Testing a Model on Coalitions in Barbary Macaque Males (*Macaca sylvanus*)

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À mes parents, Monique et René,
avec tout mon amour

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There are many things we do not dare to try because they are difficult, but they are difficult because we do not dare to try them.

Seneca

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Zusammenfassung

Menschen sind bekannt für ihre Neigung, Koalitionen und Allianzen zu bilden. Diese Eigenschaft teilen sie mit unseren nächsten Verwandten, den Primaten. Für den Begriff „Koalition“ gibt es mehrere Definitionen, aber meistens meint man damit in der Ethologie ein von mindestens zwei Individuen gemeinsam ausgehendes aggressives Verhalten gegenüber einem gemeinsamen Kontrahenten. Die limitierten Ressourcen, um welche Primatenmännchen konkurrenzieren, sind nicht teilbar (z.B. Befruchtungen), und die Möglichkeiten für nepotistische Koalitionen sind begrenzt. Daher werden Koalitionen unter Männchen nur unter speziellen Bedingungen erwartet. Diese Bedingungen, unter denen Koalitionen zwischen Männchen innerhalb einer Gruppe bei Primaten auftreten, haben Theoretiker erst kürzlich modelliert. Der Rahmen für diese Doktorarbeit wird von einem Modell geliefert, welches besagt, dass das Auftreten und die Art der Koalition vom Wettbewerb der Männchen um sexuellen Zugang zu den Weibchen bestimmt wird (Pandit & van Schaik 2003; van Schaik et al. 2004a; van Schaik et al. 2006). Derzeit ist dieses Modell noch grösstenteils ungetestet. Wir wählten Berberaffen als Studiensubjekte um folgende zwei Ziele zu verfolgen: *(1) Die genaue Untersuchung einer der wichtigsten Annahmen für das erwähnte Koalitions-Modell (und einiger weiterer Koalitions-Modelle)*, nämlich dass eine Koalition „feasible“ und erfolgreich ist, falls die Summe der Kampfstärke der Koalitionspartner grösser ist als jene ihres Kontrahenten. Zu diesem Zweck validierten wir zuerst das normalisierte David’s Score als Hauptmass für Kampfstärke; dann konnten wir dieses Mass verwenden um die „Feasibility“ besagter Annahme zu testen. Unsere Resultate zeigen, dass die Asymmetrie der Kampfstärke zwischen Koalitionspartner und Kontrahent den Erfolg von Koalitionen bei Berberaffen zuverlässig vorhersagt. Es sind jedoch weitere Untersuchungen nötig um zu bestimmen, ob eher technische oder biologische Gründe zum nicht perfekten Übereinstimmen von Daten und Modell beitragen. *(2) Die Evaluation des heuristischen Wertes des Koalitionsmodells für Berberaffen.* Dazu mussten wir zuerst die Struktur und Funktion der Koalitionen der Männchen im Zusammenhang mit deren Konkurrenz um Paarungspartner untersuchen, um die Effizienz von Koalitionen im Verhältnis zu anderen den Fortpflanzungserfolg beeinflussenden Faktoren zu setzen. Unsere Daten deuten darauf hin, dass Koalitionen hauptsächlich von Männchen mit mittlerem bis tiefem Rang in der Hierarchie und fortgeschritteneren Alters („post-prime“) gebildet werden, sowie

dass sie auf Männchen höheren Ranges und besten Alters („prime“) abzielen. Koalitionspartner können ihren Fortpflanzungserfolg erhöhen, indem sie einem Männchen ein Weibchen wegzunehmen vermögen. Berberaffen scheinen Koalitionen aber auch in Abwesenheit von Weibchen zu bilden um höherrangige Männchen einzuschüchtern, so dass diese später in der Konkurrenz um Paarungspartner geschwächt agieren. Diese Art von „all-up, leveling“ Koalitionen kam jeweils dann vor, wenn der Konkurrenzkampf um Paarungspartner auf einem geringen Niveau war, wie es vom Koalitionsmodell vorhergesagt wird. Allerdings passen nicht alle Aspekte der in dieser und anderen Studien beobachteten Koalitionen mit den Vorhersagen des Modells überein. Der starke Einfluss des Alters auf das Bilden von Koalitionen und die kleinen Koalitionsgrössen bilden Themen für künftige Untersuchungen sowohl empirischer wie auch theoretischer Art.

Abstract

Humans are well-known for their proclivity to form coalitions and alliances, and they share this characteristic with our closest primate relatives. The term "coalition" has been defined in various ways, but is most commonly defined in ethology as a joint aggression between at least two individuals against a common target. Because the limited resource primate males compete for is not shareable (i.e. fertilizations) and the opportunities for male nepotistic coalitions are limited, coalitions among males are expected only in special conditions. The conditions giving rise to within-group coalitions among primate males have only recently received theoretical attention. The model which constitutes the framework for this thesis states that the occurrence and type of coalitions observed within multi-male groups is determined by the level of sexual contest competition that males experience (Pandit and van Schaik, 2003; van Schaik et al., 2004, 2006). At present, this model remains largely untested. Using the Barbary macaque as a study system, the first of the two goals of this thesis was (1) *to closely scrutinize one of the major underlying assumptions of the coalition model and several coalition models in animals*, that a coalition's strength can be estimated as the sum of the fighting abilities of the coalition partners, and if that sum exceeds the target's strength the coalition would be feasible and thus successful. For that purpose, we first validated the normalized David's score as a cardinal measure of male competitive ability, and then used this competitive ability score to test the feasibility assumption. Our results show that the asymmetry in strength between the coalition and the target was a significant predictor of coalition success in Barbary macaques, although more work is needed to determine whether technical or biological reasons may contribute to explain the lack of perfect fit to the data. The second goal was (2) *to evaluate the heuristic value of the coalition model for Barbary macaque males.* To do so, we first had to examine the patterning and function of coalitions among males in the context of mating competition, and determine the efficacy of this tactic in relation to other factors affecting male mating success. Our data indicate that coalitions were mostly formed by mid-low ranking, post-prime males and targeted at higher-ranking, prime males. Coalitions allowed the partners to increase their mating success by usurping females from higher-ranking males. However, we found evidence

suggesting that Barbary macaque males may also use coalitions in the absence of resources to intimidate higher-rankers in showing restraint in mating competition. This type of all-up, leveling (or non-rank-changing) coalitions occurred at low-medium intensity of sexual contest competition, as predicted by the coalition model for male-male coalitions. However, not all aspects of male-male coalitions reported in this and other studies fit the predictions of the model. The strong age-related expression in coalitionary activity and the smaller than expected size of coalitions now becomes an issue to be examined both empirically and theoretically.

Chapter 1

Introduction

Humans are well-known for their proclivity to form coalitions and alliances, ranging from within-family to between-nation states (Gavrilets et al., 2008), and they share this characteristic with our closest primate relatives (see references below), as well as with some carnivores (reviewed in Zabel et al., 1992), cetaceans (Connor et al., 1992) and perissodactyles (Schilder, 1990; Feh, 1999). The term "coalition" has been defined in various ways, but is most commonly defined in ethology as a joint aggression between at least two individuals against a common target (de Waal and Harcourt, 1992, see Box 1-1). Usually, the term coalition is used for the actual interaction, whereas the term alliance is reserved for a longer-term relationship within which coalitions occur (de Waal & Harcourt 1992).

Coalitions in non-humans can occur within groups or between groups. Among modern humans, between-group coalitions that have other such coalitions as targets rather than a single individual are known as warfare. There is an increasing biologically inspired literature on its history and dynamics (reviewed in van der Dennen, 1995). Among non-humans, between-group coalitions, in which a coalition competes against another such coalition or against a single intruder, have not received much attention so far, although there are some notable exceptions (e.g. Packer, 1977; Bygott et al., 1979; Pope, 1990; Connor et al., 1992; Feh, 1999). I therefore focus on within-group coalitions.

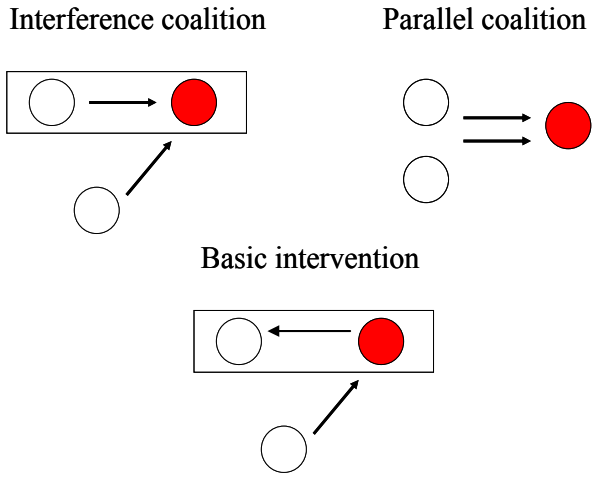
Coalitions in an evolutionary perspective

Within-group coalitions are limited in their taxonomic distribution (de Waal and Harcourt, 1992). Even in primates where they are common, it does not mean that all species display them or that both sexes form coalitions equally often. According to socio-ecological theory, competition in primates has two major objects, mates and food, which should consequently be the main objects of coalition formation (Wrangham, 1980;

Chapais, 1995). Because of the fundamental difference in the nature of the resources the two sexes compete for, coalitions are expected to be less common among males than females (van Hooff and van Schaik, 1992; van Schaik, 1996). Females compete for access to food, which are potentially shareable resources, whereas males compete for fertilizations, which cannot be shared and come in a fixed total amount (Emlen and Oring, 1977; Wrangham, 1980). Thus, coalitions among males are expected only in special conditions.

Box 1-1

Several terms can be found in the primatological literature such as "agonistic intervention", "fight interference", "support choice", etc. (de Waal & Harcourt 1992). Coalitions as defined in this study include instances where two individuals simultaneously attack the same target (parallel coalitions, e.g. savanna baboons: Noë 1986) and where one male intervenes in an on-going conflict and sides with one of the two opponents (interference coalitions, e.g. bonnet macaques: Silk 1992; Tibetan macaques: Berman et al. 2007; cf. Noë 1994). Instances where when one individual simply protects another (basic intervention) will not be called coalitions here (see also Chapais 1995). Below: the target of the aggression is shown in red; the box represents the initial aggression.



A factor that is expected to facilitate the formation of coalitions is kinship (Wrangham, 1982). Indeed, an important part of female-female coalitions in female-

bonded groups (sensu Wrangham 1980) are compatible with kin selection theory (Chapais, 1995; cf. Hamilton, 1964). However, a strong bias towards female philopatry in primates (reviewed in Smuts et al., 1987) limits the occurrence of male-male nepotistic coalitions. In chimpanzees where females emigrate and males remain in their natal community (Nishida, 1979), coalitions sometimes involve kin, such as maternal brothers (Riss and Goodall, 1977), but coalition partners are not especially likely to be close relatives (Mitani et al., 2000; Vigilant et al., 2001). Another example of coalitions among non-kin are male savanna baboons (*Papio cynocephalus*), who migrate from their natal groups and seldom associate with close male kin as adults (Bercovitch, 1988; Noë, 1986), but nevertheless form coalitions with each other to get instantaneous access to estrous females (reviewed in Noë, 1992). It was concluded that kinship cannot be expected to be a major determinant of coalitions among primate males (Chapais, 1995). The conditions giving rise to male-male coalitions in primates have only recently received theoretical attention (for a general model among females: Wrangham, 1980; van Schaik, 1989; Sterck et al., 1997; Isbell and Young, 2001), but before explaining the basis for the model that constitutes the framework for this thesis, I will begin with a review of the main characteristics of male-male coalitions in primates.

Main characteristics of male-male coalitions in primates

Coalition formation by males against rival males can only occur when there are at least three males present in a group. Thus, whenever males compete by monopolizing a group of females, resulting in one-male, multi-female groups, coalitions will necessarily be absent (reviewed in Smuts et al., 1987). In multimale groups, coalitions among males have been reported in several species (e.g. chimpanzees: de Waal, 1982; Goodall, 1986; savanna baboons: Bercovitch, 1988; Noë, 1992; bonnet macaques: Silk, 1992a; Barbary macaques: Kuester and Paul, 1992; Witt et al., 1981; Tibetan macaques: Berman et al., 2007; Assamese macaques: Ostner et al., 2008; sooty mangabeys: Bernstein et al., 1983; white-faced capuchins: Perry, 2003), but are rare or strikingly absent in many more others (e.g. rhesus macaques: Chapais, 1983a; mandrills: Setchell and Wickings, 2001; chacma baboons: Weingrill et al., 2000; red colobus: Firos, 2001). Within-taxon variability is also appreciable.

Coalitions can be variable in their composition, i.e. they can occur opportunistically on a case-by-case basis, or represent long-term alliances (Noë, 1986; Goodall, 1986). They can occur in three different configurations according to the dominance rank of the coalition partners relative to their target (all-up, bridging, all-down; van Schaik et al. 2004; cf. Chapais, 1995; Fig. 1-1). They can also produce different outcomes. Coalitions may relate directly to reproductive benefits, as when two males usurp an estrous female from a higher-ranking competitor ("all-up, leveling", cf.

van Schaik et al., 2004; e.g. Bercovitch, 1988; Noë, 1992; Thierry, in press). Alternatively, coalition formation may directly affect dominance status and indirectly modulate reproductive success by allowing lower-rankers to increase their rank and control access to resources ("all-up, rank-changing", cf. van Schaik et al., 2004; e.g. de Waal, 1982; Nishida, 1983). Another type of coalitions that has to date only been described in one population of chimpanzees consist in coalitionary mate guarding by higher-ranking males (Watts, 1998).

Modeling coalitions

So far, there have been few quantitative models of coalition formation in general. Dugatkin and Johnstone (Dugatkin, 1998; Johnstone and Dugatkin, 2000) examined how winner and loser effects can affect the likelihood that coalitions among two individuals against a third will be formed. This model has not received much empirical attention so far (but see Jennings et al., 2009), probably because most work on winner and loser effects has focus on rodents, fish and birds where coalitions are not observed (Dugatkin 1998 and references therein). Whitehead and Connor proposed a general model to explain how large alliances in fission-fusion societies (e.g. bottlenose dolphins) should be (Whitehead and Connor, 2005) and how the rate at which individuals encounter one another influences their propensity to form coalitions (Connor and Whitehead, 2005). Most recently, Mesterton-Gibbons and Sherratt (2007) proposed a game-theoretic analysis of coalition formation in animals which aimed at identifying the circumstances in which a coalition of 2 versus 1 is most likely to arise. Gavrilets et al. (2008) proposed a flexible theoretical approach that he used to study the conditions under which intense competition for a limiting resource can lead to the emergence of a single leveling alliance including all members of the group, a phenomenon that is commonly observed in human hunter-gatherers but strikingly absent in non-human primates (Boehm, 1999). However, at present, these general models cannot explain the observed diversity in male-male coalitions depicted above, suggesting that more specific models are needed for now.

The first, ad hoc model specifically dealing with primate coalitions was developed by Noë (1994). This descriptive model aimed at explaining the observation that only a subset of males that occupy middle or lower ranks frequently form coalitions, while the highest and lowest ranking males are little involved in coalition formation (reviewed in Noë, 1992, table 11.1). Noë estimated male fighting ability from ordinal rank and delimitated the sets of pairs that would be able to form successful coalitions against a single target. The main conclusion was that males of intermediate fighting ability are more likely to be seen in coalitions since the number of potentially successful partner-target combinations is highest for those males. (See also Noë 1990 for a challenge to the use of the Prisoner's Dilemma model as a paradigm for coalition formation in savanna

baboons.) Building on this, the most concrete attempt in explaining the variability in male-male coalitions is the model recently developed by van Schaik and colleagues (Pandit and van Schaik, 2003; van Schaik et al., 2004, 2006), which states that the occurrence and type of coalitions observed within multi-male groups is determined by the level of sexual contest competition that males experience (i.e. β parameter introduced by Pandit and van Schaik, 2003). For the sake of convenience, in this thesis we use the term "coalition model" to refer to the Pandit/van Schaik model, or indicate it otherwise.

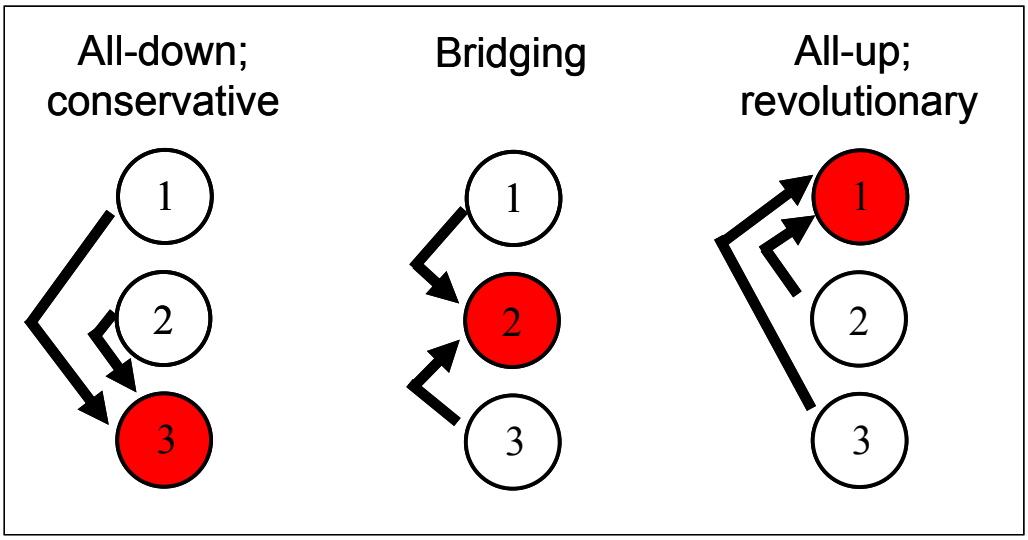


Figure 1-1 Schematic representation of the basic configurations of within-group coalitions (modified from van Schaik et al. 2006; cf. Chapais 1995). Top-ranking male occupies rank 1. Arrows indicate the direction of the attack; the target is shown in red.

A model for within-group coalitions among primate males

The model is based on the premise that the general goal of male behavior is to maximize fitness. Its basic approach is to identify the conditions in which within-group coalitions with a single target are both *profitable* and *feasible*. A coalition is profitable if for each coalition member, the direct benefits in terms of increase in fitness exceed the costs in terms of reduction in fitness (e.g. through the risk of injury, energy expenditure, etc.). In order to identify the conditions for profitability, the relationship between fitness and dominance rank must be determined. It is assumed that males in a primate group compete through priority-of-access (cf. Altmann, 1962) for a constant-sum resource, i.e. the number of fertilizations in a given time period. As a consequence, the relationship between payoffs and rank is inevitably concave (at best approaching linearity, Fig. 1-2).

This curve can be characterized by a single parameter, β, which is the proportion of resources available to a male that can be monopolized and usurped by him. We will postpone the discussion of how to estimate β until Chapter 6. Coalitions can be profitable in two very different ways, i.e. they can be rank-changing or leveling (see examples above). Only leveling coalitions affect the value of β, because they reduce monopolization potential by the top-rankers (Fig. 1-3). We will come back to this point in Chapter 6.

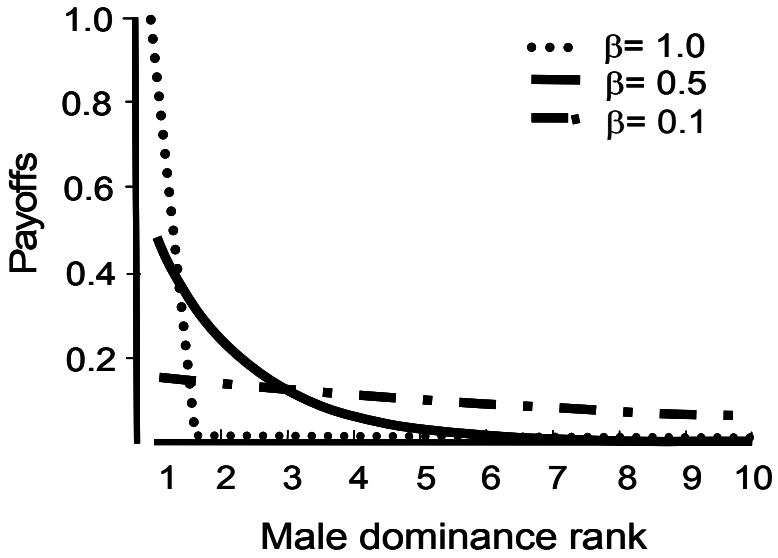


Figure 1-2 Relationship between payoffs and rank for males in a primate group competing through priority-of-access (cf. Altmann, 1962) for constant-sum resources. The curve can be characterized by a single parameter, β, which is the proportion of resources available to a male that can be monopolized and usurped by him. β is expected to be highest (β →1) where females mate asynchronously and preferentially mate with dominant males, and lowest (β → 0) when females estrous cycles overlap to a large extent and females mate promiscuously (see Chapter 6).

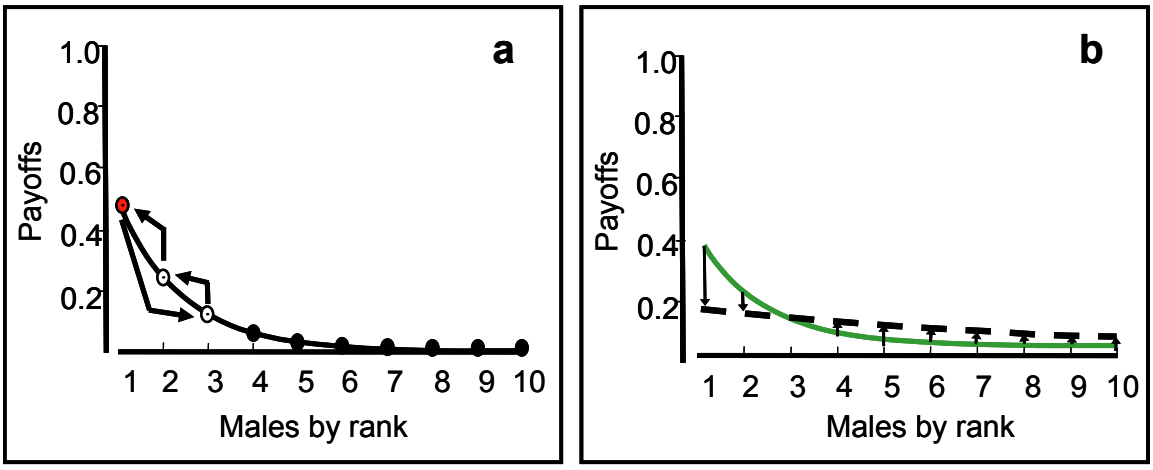


Figure 1-3 All-up, rank-changing (a) and all-up, leveling (b) variant of coalitions considered in the model (modified from van Schaik et al. 2006).

Feasibility needs to be estimated as well. A coalition is feasible if the strength of the coalition (i.e. the sum of the fighting abilities of the coalition partners) is more than the strength of their target (cf. Noë, 1994). In the actual version of the model, the authors use as a simplifying assumption that fighting ability and payoffs show a similar functional form with rank, so payoffs are used instead of fighting ability to estimate coalition strength in the model (Fig. 1-4). In a more recent (unpublished) version of the model, fighting ability of individuals is assumed to follow a distribution with rank that is of the same shape as the payoff curve but not identical to it, because it is assumed that this curve is always less steep than the payoff curve. This modification does not change the qualitative predictions of the model (S. Pandit & C. van Schaik, pers. com.). When coalitions are both feasible and profitable, coalitions are viable and thus expected to occur.

Predictions

The model makes a number of testable predictions concerning the range of β values (or level of monopolization potential) in which different types of coalitions are expected to occur, which males are expected to participate, etc. The basic predictions of the model are presented in Table 1-1. It is easy to see that under complete scramble (i.e. $\beta \rightarrow 0$, i.e. the distribution of payoffs according to rank is flat) monopolization of fertile females may be difficult or impossible, so coalitions do not pay and should not occur. The profitability of all-up coalitions increases with increasing monopolization potential (i.e. as the shape of the curve becomes steeper) and are expected at low-medium levels of β (i.e. < 0.5). All-up rank-changing coalitions need to generate sufficient benefits to

permanently change the rank position of the partners and are predicted to occur at higher contest levels than leveling coalitions. When contest is too high (i.e. $\beta > 0.5$), all-up coalitions are still profitable but are no longer feasible, and only the bridging rank-changing type among relatives is expected (which are always feasible, and profitable if the male receiving the coalitionary support is a relative of the helping male). If no relatives are at hand, no coalition should be observed.

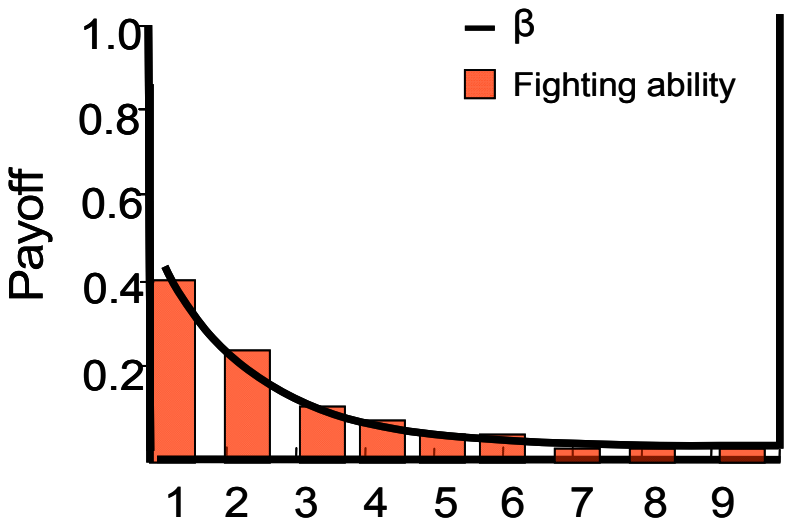


Figure 1-4 The coalition model assumes that fighting ability and payoffs show a similar functional form with rank.

Table 1-1 Basic predictions of the coalition model

β (contest)	Coalition configuration	Coalition outcome	Rank of partners	Partners are kin?	Rank of target	Coalition size
High-Very high	Bridging (or no coalitions)	Leveling/Rank-changing	Top and High	Yes	High	Small
Medium	All-up	Rank-changing	Below top	Not necessarily	High	Small
Low-Medium	All-up	Leveling	Mid-low	Not necessarily	High	Large
Very low	No coalitions	-	-	-	-	-

Aims and organization of this thesis

At present, the Pandit/van Schaik model remains largely untested (but see: van Schaik et al., 2004; Jones, 2005). I had two goals:

1. *To closely scrutinize one of the major underlying assumptions of several coalition models in animals*, that a coalition's strength can be estimated as the sum of the fighting abilities of the coalition partners, and if that sum exceeds the target's strength the coalition would be feasible and thus successful.This is the asymmetry in strength hypothesis of Noë (1994; see also Whitehead and Connor, 2005; Mesterton-Gibbons and Sherratt, 2007). The two first papers in this thesis are concerned with testing this feasibility assumption. Although there is some indirect empirical evidence supporting this assumption in primate males (Bercovitch, 1988; Noë, 1994; Noë and Sluijter, 1995; Silk, 1992b), a major impediment for detailed empirical investigation of the role of fighting ability in coalitionary contests is the lack of a quantitative measure of fighting ability that would allow the assessment of the *combined* fighting ability of the coalition partners (or coalition strength) in relation to their target. Thus, I first start by validating a cardinal measure of competitive ability in Barbary macaque males (Chapter 2), and then use this measure to test the feasibility assumption (Chapter 3). As mathematical cost-benefit models should not be confused with the way animals make behavioural decisions (Marsh, 2002), I also assess in Chapter 3 whether male coalitional decision-making is based on asymmetry in strength.

2. *To evaluate the heuristic value of the coalition model for Barbary macaque males.* To do so, I first had to examine the nature and function of coalitions among males in the context of mating competition, and determine the efficacy of this tactic in relation to other factors affecting male mating success. Data on male-male coalitions in Barbary macaques in the context of mating competition are scarce (see below), but current evidence suggests that males may form all-up, leveling coalitions during the mating season (Kuester and Paul, 1992). In contrast to savanna baboons where coalitions are often (but not always) used by subordinate males to usurp females from more dominant males (reviewed in Noë 1992), Barbary macaque males often appear to use coalitions in the absence of resources. It has been suggested that males may use coalitions to intimidate higher-rankers in showing restraint in mating competition (Kuester and Paul, 1992; Paul et al., 1993). In chapter 3, I describe the patterns of coalition formation among males and their context of occurrence, and test some predictions derived from the intimidation hypothesis.

The fourth chapter focuses on the effect of coalitions and female behavior on male mating success. I use the priority-of -access model (cf. Altmann 1962) to set the basic expectation of mating skew among males, and compare it to the observed distribution of matings in the study group. A detailed analysis of the tactics used by males and females in the context of changeover in consortships allows me to determine the extent to which coalition formation contributes to leveling mating access.

These four chapters (2-5) constitute the core of the thesis. As I wanted each chapter to stand on its own, I allowed some overlap of material between chapters. In the final chapter (6), I discuss the heuristic value of the coalition model as applied to Barbary macaque males, present some limitations reported in this and other studies and suggest some future directions for research.

Barbary macaques as a study system

Barbary macaques represent an interesting species in which to test the heuristic value of the coalition model. They live in multi-male multi-female groups (Fooden, 2007). Their species-specific characteristics such as a seasonal breeding (e.g. de Turckheim and Merz, 1984; Fa, 1986) and a promiscuous mating system (Small, 1990; Kuester and Paul, 1992) should translate into a relatively low potential for male monopolization, which are the very conditions under which the model predicts the occurrence of all-up coalitions.

So far there exists no detailed work on coalition formation in Barbary macaques, and when coalitions were described it was in the framework of studies on another topic (Witt et al. 1981; Kuester and Paul 1992; Kuester and Preuschoft unpublished manuscript). Coalitions have been reported to be rare or absent in certain groups (Taub 1980), although the reasons for this intra-species variability is completely unknown. Unfortunately, the only study entirely dedicated to the topic of coalitions most likely dealt with a special phenomenon called “scream-fights” which is only known to occur among Barbary macaque males and not in any other species (Widdig et al., 2000, see the definition of coalition given by the authors, p. 40). Scream-fights are long-lasting and noisy events characterized by two primary antagonists screaming at each other and third parties joining the conflict as a response. Scream-fights are the exclusive domain of post-prime males. Interventions in scream-fights are mostly de-escalated (i.e. directed screaming and inhibited or ritualized biting often accompanied by clasping; Fig. 1-5), and thus can often not be qualified as interference coalitions (or aggressive acts of support) in a strict sense (A. Bissonnette & S. Preuschoft, in prep.). In the current study, I focus on “regular” coalitions, i.e. a joint aggression between at least two individuals against a common target, which occurred outside the context of scream-fights and are more typical

of other species (Fig. 3-4). The phenomenon of scream-fights will be treated in details elsewhere.

The present study was conducted on two groups of Barbary macaques living under semi-free ranging conditions. The first part of the field work was conducted during the mating season 2005/06 in the Wildpark Daun (Germany), and the second part of the study during the mating season 2006/07 in the Affenberg Salem (Germany). Coalitions occurred at a very low rate in the Daun group, so most of the data presented in this thesis comes from the Salem group. I use the data (or its absence) from the Daun group to discuss the overall validity of the coalition model in Chapter 6.

Figure 1-5 A scream-fight among Barbary macaque males.

Chapter 2

A cardinal measure of competitive ability in Barbary macaque males

Cardinal scores of individual competitive ability allow us to quantify the magnitude of the difference between the competitive ability of any two individuals. However, they have rarely been used in animal behavior because most researchers were mainly interested in ordinal ranking. In this paper, we validated the normalized David's score (David 1987; de Vries et al. 2006) as a cardinal measure of male competitive ability in a group of Barbary macaques living under semi-free ranging conditions. To derive competitive ability scores, we used a semi-experimental protocol where two males had to compete over access to a prized food resource (i.e. a nut) within the natural group setting. This protocol was used because it allowed the exclusion of three factors other than competitive ability (i.e. respect of ownership, social tolerance and motivation) which may influence the outcome of dyadic encounters in group-living primates. We expected that a measure of competitive ability excluding the three above-mentioned influences would correlate with some intrinsic features of males. Male competitive ability scores were calculated based on 357 nut tests. As expected, male competitive ability shows a curvilinear relationship with age (used as a proxy for male general physical condition), with young, "athletic" males having the highest scores. However, we also found that male competitive ability scores were highly correlated with the dominance scores derived from naturally occurring agonistic interactions, which suggest that observations of spontaneous interactions may suffice to estimate the competitive abilities of individuals. We conclude that despite its limitation, the normalized David score is often preferred to ordinal ranking as an estimate of RHP (resource holding potential) as originally defined by Parker (1974).

Bissonnette A., Lange E., van Schaik C.P. Ethology (2009)

Introduction

Ordinal measures of competitive ability are widely used in animal behavior studies. Generally, behavioral information is collected and arranged in a dyadic interaction matrix in which the individuals are ordered following some conventional method. One commonly used method consists in reorganizing the individuals in the interaction matrix such that some numerical criterion, calculated for the matrix as a whole, is minimized or maximized (de Vries, 1998; de Vries and Appleby, 2000), thus yielding an ordinal rank order. Another type of method has also been described, where overall individual success is calculated (Gammell et al., 2003; Hemelrijk et al., 2005; reviewed in de Vries et al., 2006). This latter method has a major advantage, in that it provides a measure that allows to quantify the magnitude of the difference in competitive ability between two individuals. For example, a cardinal measure reflects the observation that the difference in competitive ability between A and B is larger than between B and C when A beats B in all encounters whereas B beats C in two-third of the encounters, whereas ordinal measures do not reflect this important aspect of the data (cf. Boyd and Silk 1983; Fig. 2-1).

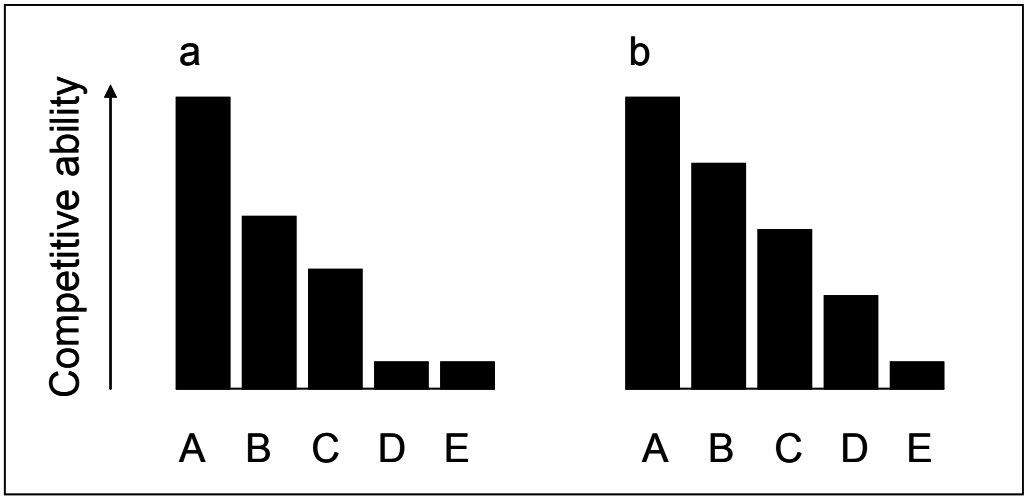


Figure 2-1 A cardinal measure (a) reflects the observation that the difference in competitive ability between A and B is larger than between B and C, and would allow the males D and E to occupy the same competitive ability "slot", whereas ordinal measures do not reflect this important aspect of the data (b).

Yet, the cardinal score *per se* has rarely been used in animal behavior studies, especially in primatology, where the use of ordinal ranking is a well-established tradition (but see e.g. Boyd and Silk, 1983; Fa, 1986; de Vries et al., 2006; Ostner et al., 2008). Here, we validate a cardinal measure of male competitive ability in Barbary macaque males based on the normalized David's score (de Vries et al., 2006; David, 1987).

We define competitive ability as the "ability of an animal to claim a resource by means of force or the threat of force" (cf. de Waal, 1989, p. 246). The problem of deriving a cardinal estimate of individual competitive ability has two main components, the first one being the choice of the cardinal estimate *per se* and the second one the choice of the raw material used to derive this estimate. Rating systems for paired comparison data are widely available in the literature (reviewed in Andrews and David, 1990; Albers and De Vries, 2001). We chose the David's score (David, 1987) as an estimation of a male's relative competitive ability, because it shows various desirable properties (see also Gammell et al., 2003; Hemelrijk et al., 2005; de Vries et al., 2006). First, the ratings are directly comparable among the contestants of the same group, which means that two group members with the same rating are likely to have a similar "competitive ability". Second, the David's score has been specifically developed for ranking objects in an incomplete or otherwise unbalanced paired-comparison tournament, where pair-wise data are not available for all possible dyads (David, 1987) and is thus robust against missing data (Douglas M. Andrews, personal communication). Third, being a non-parametric score it does not require that the rather severe assumptions necessary for other cardinal measures of competitive ability be satisfied and does not assume transitivity (e.g. Boyd and Silk, 1983). This last property is important, because a measure of competitive ability should not assume a linear order where one top ranking individual is stronger than all others, a second ranking individual is stronger than all others except the top one, and so on, but should allow two individuals to occupy the same competitive ability "slot" (Fig. 2-1).

To derive individual competitive ability scores, one would ideally observe individuals competing against each other in purely dyadic situations. One direct and efficient way to collect reliable data would be to design a tournament, whereby each individual is experimentally induced to compete against other individuals in a series of paired encounters. This experimental protocol was successfully used among non-familiar individuals in studies of arthropods, fishes and reptiles (e.g. Austad, 1983; Sneddon et al., 2000; Wong, 2004; Stuart-Fox et al., 2006), but obvious ethical and logistical restrictions do not allow researchers to use such a protocol in many other organisms, such as primates. Here, we propose an alternative. It consists in a simple semi-experimental protocol where the study animals compete among themselves in a dyadic fashion to get access to an indivisible prized food item (here: a peanut), but do so within the group. We knew from a previous work that familiar Barbary macaque males were very unlikely to use physical aggression over access to peanuts (Preuschoft et al., 1998). A second

alternative would be to use naturally occurring agonistic interactions, but we think that the semi-experimental protocol may be preferred for the following reasons. First, winners and losers can always be identified unambiguously, in contrast to situations where no resource is directly at stake. Second, the animals are tested in a standardized setting and the data can be accumulated relatively rapidly. Finally and most importantly, the protocol is designed to allow the exclusion of factors other than competitive ability that might influence the outcome of the encounters (see below), while this is generally not possible with naturally occurring agonistic interactions. In this paper, we compare the competitive ability scores derived from the peanut tests to those derived from dyadic agonistic interactions, in order to determine the extent to which naturally occurring interactions are affected by the three factors mentioned below.

In assessing a male's competitive ability, it is important that we can exclude the effects of confounding factors that may affect the outcome of dyadic encounters. The factors that determine dyadic contest outcome for any given species depend on the precise circumstances of the contest. In group-living primates, de Waal (1989) identified three such factors. These are: (i) the inhibition to contest a resource already possessed by another individual (i.e. respect of ownership, cf. Kummer, 1973; Maynard Smith and Parker, 1976), (ii) social tolerance and (iii) motivation levels (or one's lack of readiness to use one's competitive ability). In this study, we dealt with these three factors in the following way. First, respect of ownership of an asymmetrically placed peanut (e.g. an inferior rival eats the nut that is lying closer to him) was previously described among Barbary macaque males (Preuschoft and Paul, 2000). We controlled for this possible confounding factor by placing the peanut equidistant between the males, so we will henceforth ignore it. Second, de Waal (1989) originally described tolerant relationships in a group of rhesus monkeys where animals were observed to compete over a shareable resource (i.e. access to a water basin), and defined social tolerance as a "low competitive tendency, especially by dominants towards subordinates". Here, we used a indivisible resource and assume that the likelihood that social tolerance would be expressed by the stronger rival is very low, since being tolerant would not mean sharing the resource with another individual but giving it away altogether. Third, a pilot study conducted by one of the authors revealed that individual males were almost always motivated to eat the peanut, and showed a preference for this incentive over other types of food items such as fruits, vegetables or grains (A.B., own obs.). Consequently, we expected the motivation factor to have at best a low impact on the outcome of the tests. Motivation tests were nevertheless performed in order to assure that the rivals were interested in the incentive.

We expected that a measure of competitive ability excluding these three influences would correlate with some intrinsic features of males such as body mass, body size, age, weaponry (etc.), as those factors have been shown to be important in deciding dyadic encounters in organisms as diverse as insects, crustaceans and mammals (e.g. Caldwell and Dingle, 1979; Austad, 1983; Clutton-Brock et al., 1979; Yamane et al.,

1996). As a first step, we used male age as a proxy for male general physical condition and investigated its relationship with the competitive ability scores.

Methods

Study species and study group

Barbary macaques live in multi-male multi-female groups and are considered highly seasonal breeders (van Noordwijk and van Schaik, 2004b, table 12.1). The study was conducted by A.B. and Elena Lange during the mating season 2006/07 (September to mid-February) at the Affenberg Salem (Germany), on one large-sized group of Barbary macaques, which inhabited a forested enclosure of 14.5-ha (for a history of the colony, see de Turckheim and Merz, 1984). The study group (H) was composed of 27 adult females (> 5 years old), 7 prime males (aged between 7 and 12 years old), 17 post-prime males (≥ 14 years old) and 6 juveniles. All adult animals were recognized individually and habituated to the observers. Animals were fed once daily with fruits, vegetables and grains, which were distributed in different areas within the park. The monkeys also fed extensively on natural vegetation, including leaves, herbs, grasses and bark. Water was available *ad libitum*. From March to November tourists were allowed into the park, but were restricted to a path.

Peanut tests

The protocol used in this study was modified from Preuschoft *et al.* (1998). Peanut tests were performed opportunistically by E. L. (95% of all tests) and A.B. (5%). Each test consisted of throwing a nut between two adult males (hereafter rivals). Tests were considered for further analysis if they fulfilled all of the following three conditions: (1) The rivals were sitting within 10-15 meters of each other and were paying attention to the observer (i.e. the observer cracked the nut to get males' attention), (2) no male was present in the imaginary circle whose diameter is the line connecting the rivals, although females and juveniles (which are subordinates to all adult males) were occasionally allowed within that circle if they were sitting at least two meters away from the peanut (Fig. 2-2); and (3) the peanut was equidistant between both rivals. To assure equidistance the experimenter stood within 2 meters of the imaginary line connecting the males and positioned herself at equal distance between the opponents before dropping the nut. Four tests where the nut laid closer to rival A but was eaten by rival B were also included. The identity of all third parties in sight (hereafter bystanders) was recorded according to their distance to the peanut (≤10 m, ≤20 m, ≤30 m and >30m). According to their outcomes,

the tests were classified into two mutually exclusive categories: a test was either (1) "decided" when one rival ate the nut or (2) "tied" when none of the rivals ate the nut, because a third party snatched the nut away.

Behavioral data

Behavioral observations were conducted daily by A.B., E.L. and Nicole Bischofberger. A total of 279 hours of male focal data (Altmann, 1974) was collected by A.B. In addition, *ad libitum* sampling (Altmann, 1974) was done by all observers throughout the day, whereby detailed information on agonistic interactions among adult males were recorded. Dyadic aggressive acts (open-mouth threat, lunge at, chase, slap, grab, bite) and approach/retreat interactions were used to construct the agonism matrix (see Appendix B for behavioral definitions). If an agonistic interaction turned into a polyadic interaction, only the sequence preceeding the intervention of a third-party was considered. 5.5% of all dyadic interactions were bidirectional (i.e. both individuals behaved aggressively in a given interaction): these interactions were considered as a "tie" and entered in the interaction matrix as explained below. The percentage of agreement (cf. Martin and Bateson, 2000) for focal sampling between A.B. and N.B., and A.B. and E.L. reached at least 80%.

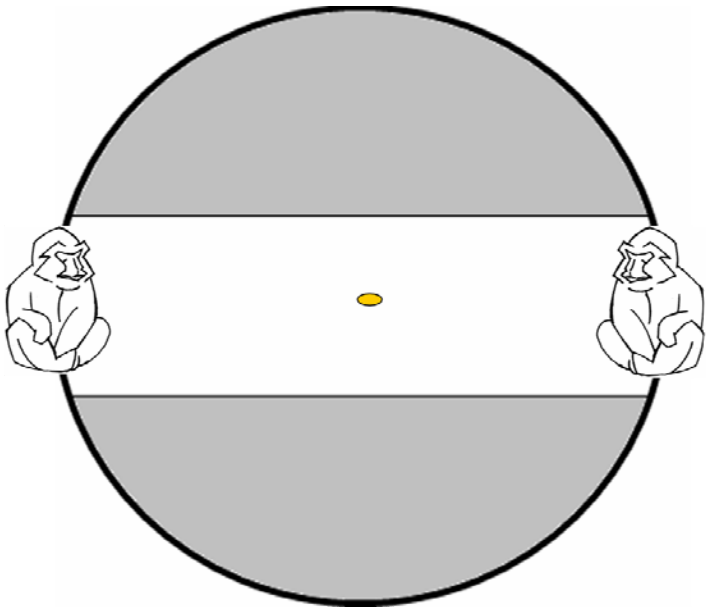


Figure 2-2 Test zone. No adult male other than the tested males was allowed within the imaginary circle. Females and juveniles were exceptionally allowed within that circle, but only if they were sitting at least two meters away from the peanut (i.e. outside the region between the parallel lines, in the shaded zones).

David's score

The procedure for calculating competitive abilities based on the David's score (DS) is as follows. First, the dyadic proportions of wins are calculated. The proportion of wins by individual *i* in his interactions with another individual *j* (P_{ij}) is the number of times that *i* defeats *j* (α_{ij}) divided by the total number of interactions between *i* and *j* (n_{ij}), i.e. $P_{ij}=\alpha_{ij}/n_{ij}$. A tied encounter counts as half a win (and half a loss) for both rivals (David, 1987). If *i* and *j* are not compared (i.e. if $nij=0$), both P_{ij} and P_{ji} are zero (David, 1987). The proportion of losses by *i* in its interactions with *j* is $P_{ji}=1-P_{ij}$. DS for each member, *i*, of a group is calculated with the formula:

$$DS=w+w_2-l-l_2$$

where *w* represents the sum of *i*'s P_{ij} values, w_2 represents the summed *w* values (weighted by the appropriate P_{ij} values) of those individuals with which *i* interacted, *l* represents the sum of *i*'s P_{ji} values and l_2 represents the summed *l* values (weighted by the appropriate P_{ji} values) of those individuals with which *i* interacted.

Second, to obtain a distribution of scores ranging between 0 and N-1, the David's score was converted into a normalized David's score (NormDS) following the formula suggested by de Vries *et al.* (2006) as follows:

$$NormDS = \{DS + MaxDS(N)\}/N = \{DS + N(N-1)/2\}/N$$

where MaxDS(N) is the highest potential David's score that can be obtained by an individual in a group of size N (for more mathematical details see David, 1987; de Vries et al., 2006)

Motivation

In this paper, motivation is defined as the willingness of an animal to obtain the peanut. Motivation was estimated in two ways. First, the motivation of the defeated rival was determined in specific "motivation tests", whereby a second peanut was thrown within 5 meters (i.e. out of arm reach) of the loser right after- or within 5 minutes following the end of the test. These motivation tests were only performed when no other male (including the rival) was present within 20 meters. In order to avoid a decrease in competitiveness in real tests after repeated exposure to motivation tests (e.g. through habituation), we performed motivation tests unsystematically and at a low rate, and avoided testing the same males on consecutive days. Second, we performed general

"motivation tests" at the end of the data collection period, whereby a peanut was thrown within 5 meters of a male and when no other male was present within 20 meters. The 24 adult males were tested once in each of these three time periods: (1) before the morning feeding session, when the animals were most likely to be hungry, (2) at mid-day when the animals were resting and (3) at the end of the day when the animals resumed foraging (N=72 tests). The latency from throwing the nut by the observer to cracking the nut by the male was recorded to the nearest second.

Statistical analyses

Pearson correlations and the nonlinear function were calculated using the Software JMP 7.0. We checked for the presence of outliers in the nonlinear regression by looking at the presence of unusually large studentized residuals (Quinn and Keough, 2002). All continuous variables were tested for normality with the Shapiro-Wilk test before performing the analyses. The significance level alpha was set to 0.05.

Results

A total of 357 tests were conducted, 331 of which were "decided" and 26 of which were "tied". Of all possible male-male dyads 67.8 % (187/276) were tested at least once (median: 1, range 1-4). Males were tested against 25-86 % of their potential rivals (mean: 60%). 57.4% (205/357) of the tests were performed in post-prime male dyads, 37% (132/357) in prime/post-prime male dyads and 5.6% (20/357) in prime male dyads. Prime males spent a higher proportion of their time in the trees in comparison to post-prime males during the study period and apparently avoided each other's proximity (unpublished data), which explains the low percentage of tests conducted within this age-class. Table 2-1 shows the test matrix with calculated w, w_2, l, l_2 values and the resulting David's score and normalized David's score for the 24 adult males calculated from the 357 tests.

Effect of motivation

We hypothesized that the relative state of motivation of the rivals might affect the outcome of the peanut tests, for example if the weaker rival is more motivated than its opponent and wins the encounter as a result. Specific motivation tests were performed after 10.4% (37/357) of the peanut tests and the defeated rival ate the nut 97.3% (36/37) of the time. This suggests that the defeated rival was motivated to eat the nut, but refrained from doing so in the presence of a rival. Identical results were obtained in

general motivation tests, where the peanut was eaten by all the males in 95.8% (69/72) of the cases. The mean latency from throwing the nut by the observer to cracking the nut by the male was 1 ± 3 seconds (i.e. males generally got up immediately, walked towards- and ate the nut). Thus, we can conclude from these results that males were generally motivated to compete for the incentive, and exclude motivation as a confounding variable influencing the estimation of male competitive ability.

Relationship between competitive ability and male age

If the measure proposed here truly reflects male competitive ability, we would expect the individual scores to correlate with some intrinsic features of the males. We used male age as a proxy for male general physical condition and investigated its relationship with the competitive ability scores. Visual inspection of the scatter plot suggested a curvilinear relationship between competitive ability and male age (Fig. 2-3). A quadratic function provides a good fit to the data (R square adjusted: 0.44, $F(2,21)= 8.2$, $p=0.002$), which is better than a linear model (R square adjusted: 0.25, $F(1,21)= 8.01$, $p=0.01$). The exclusion of the only outlier (marked by a cross on Fig. 2-3) with a high studentized residual (2.74) resulted in an improved fit of the quadratic model (R square adjusted: 0.64, $F(2,20)= 17.55$, $p<0.0001$). The curve shown in Fig. 2-3 is based on the model without the outlier. Age explains 64% of the variation in competitive ability scores.

Competitive scores from nut tests and spontaneous agonistic interactions

We then compared the competitive ability scores derived from the peanut test matrix to the scores derived from the dyadic agonistic interactions that occurred naturally within the group setting. We could not control for possible confounding factors influencing the outcome of agonistic interactions (see above), but a good fit between both measures would suggest that these effects are generally weak. The agonistic matrix comprised 469 interactions, which represented 63.77% of all male-male dyads. Males were observed interacting agonistically with 37.5-83.3 % of their potential rivals (mean: 59.4%). Spontaneous submission (i.e. approach/retreat interactions) constituted 29.3% (139/469) of all agonistic interactions. Only 13 physical fights were witnessed during the study period. Figure 2-4 compares the David's Scores among males calculated from the peanut test matrix with those calculated from the behavioral matrix. Their values are highly correlated (Pearson $r= 0.724$, $p<0.0001$, $n=24$), suggesting that the competitive ability scores derived from natural agonistic interactions are a good approximation of those obtained with a semi-experimental protocol in this study group.

Table 2-1 Matrix of proportions of wins (Pij) and the values for w, w_2 l and l_2 used to calculate the David score (DS) and the normalized David's score (NormDS)

	yak	pun	leo	hul	blo	wme	fli	ron	war	Lud	neo	fro	sil	pen	ful	pin	fln	eyb	joh	fug	tec	ber	luc	cha	W	w2	DS	NormDS
yak	*	0.69	0	0.5	0	1	0	0	0	0	0	1	1	0	1	1	0	1	0	0	1	1	0	1	10.19	73.15	79.87	14.83
pun	0.31	*	1	0.5	0	0	0	0.25	1	0	0	1	1	0	1	1	0	1	0	1	1	0	1	0	11.06	80.74	77.80	14.74
leo	0	0	*	0	1	0.67	0.8	0	0	0	1	0	0	1	0	1	1	0.75	0	1	0	1	0.75	1	10.97	79.81	74.21	14.59
hul	0.5	0.5	0	*	0	0	0	0.25	0	0	0	1	1	0	1	1	1	0.5	0.75	0	1	1	1	1	11.50	68.82	55.98	13.83
blo	0	1	0	0	*	1	0.5	0	0	0	0	1	1	0.7	0	0	1	1	0	1	1	1	1	1	12.20	80.33	54.01	13.75
wme	0	0	0.33	0	0	*	0.33	0.5	1	1	1	0	1	0	1	0	0.5	0.5	1	1	1	0	1	1	12.16	75.77	50.55	13.61
fli	0	0	0.3	1	0.5	0.67	*	0	0.5	0	0.3	0	0	1	0.5	1	0.75	1	0	0	0	1	1	1	10.52	76.09	37.35	13.06
ron	0	0.75	0	0.75	0	0.5	1	*	0	0	0	0	0.2	0.5	1	0.5	0.7	1	0	1	0.5	0.5	0.83	1	10.73	75.94	34.77	12.95
war	0	0	0	0	0	0	0.5	0	*	0	1	0	0	0	1	1	0	1	0	1	0	0	1	1	7.50	47.61	28.59	12.69
lud	0	0	0	0	0	0	1	0	1	*	0	0	0	1	0	0	0	0	0	1	0	0	1	1	6.00	35.64	26.35	12.60
neo	0	0	0	0	1	0	0.7	0	0	0	*	1	0.5	0	1	0.5	0	0	1	1	0	1	1	0.5	9.20	59.75	22.62	12.44
fro	0	0	0	0	0	0	1	0	0	0	0	*	0	0	0.5	1	0	0	1	1	1	1	0	0	6.50	39.35	7.79	11.82
sil	0	0	0	0	0	0	1	0.8	0	0	0.5	1	*	0	0	1	0.75	0.38	1	1	0	1	0.5	1	9.93	62.92	7.26	11.80
pen	0	0	0	0	0.3	1	0	0.5	0	0	1	0	1	*	0	0	0	0	0.5	0.5	1	1	1	0.8	8.60	54.32	1.23	11.55
ful	0	0	0	0	1	0	0.5	0	0	0	0	0.5	1	0	*	0.5	0	0.5	0.75	0	1	1	1	0	7.75	50.08	0.19	11.51
pin	0	0	0	0	1	0	0	0.5	0	0	0.5	0	0	1	0.5	*	0	0	0	1	1	1	1	1	8.50	49.61	-7.04	11.21
fln	0	0	0	0	0	0.5	0.25	0.3	1	1	0	0	0.25	0	0	1	*	0.5	0	0	0.75	0	1	0	6.55	43.92	-7.28	11.20
eyb	0	0	0.25	0.5	0	0.5	0	0	0	0	0	0	0.63	1	0.5	0	0.5	*	0.5	0.5	0.5	0.5	1	1	7.88	47.82	-22.17	10.58
joh	0	0	0	0.25	0	0	0	1	0	0	0	0	0	0.5	0.25	0	0	0.5	*	0	1	0	1	0	4.50	27.90	-33.20	10.12
fug	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0	1	0.5	1	*	0	1	1	1	6.00	26.06	-48.62	9.47
tec	0	0	0	0	0	0	0	0.5	0	0	0	0	0	0	0	0	0.25	0.5	0	0	*	0.25	0	0.7	2.20	12.65	-85.92	7.92
ber	0	0	0	0	0	0	0	0.5	0	0	0	0	0	0	0	0	0	0.5	0	0	0.75	*	1	1	3.75	13.98	-86.38	7.90
luc	0	0	0.25	0	0	0	0	0.17	0	0	0	0	0.5	0	0	0	0	0	0	0	0	0	*	1	1.92	10.63	-131.58	6.02
cha	0	0	0	0	0	0	0	0	0	0	0.5	0	0	0.3	0	0	0	0	0	0	0.3	0	0	*	1.10	7.84	-136.39	5.82
l	0.81	2.94	2.13	3.50	4.80	5.84	7.58	5.27	4.50	2.00	5.80	6.50	9.08	7.50	9.25	10.50	7.45	11.13	7.50	12.00	12.80	13.25	18.08	17.00				
l_2	2.66	11.06	14.44	20.85	33.72	31.54	41.68	46.63	22.02	13.29	40.53	31.56	56.51	54.19	48.39	54.65	50.30	66.74	58.10	68.68	87.97	90.85	126.05	128.33				

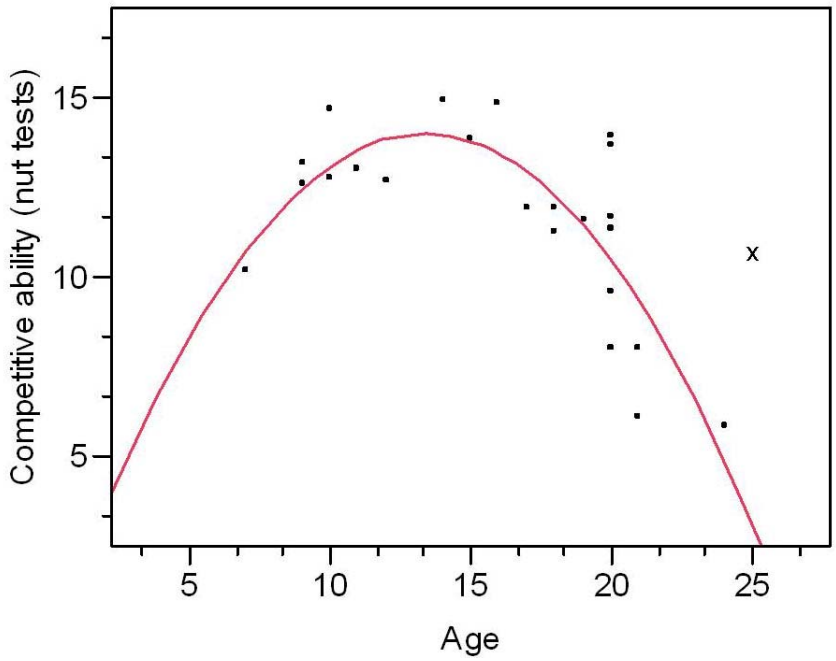


Figure 2-3 Inverse curvilinear relationship between competitive ability and age of adult males (y= 20.56 -0.45age – 0.08 (age-16.13)^2; the only outlier, marked by a cross, was not included in the calculation of the curve).

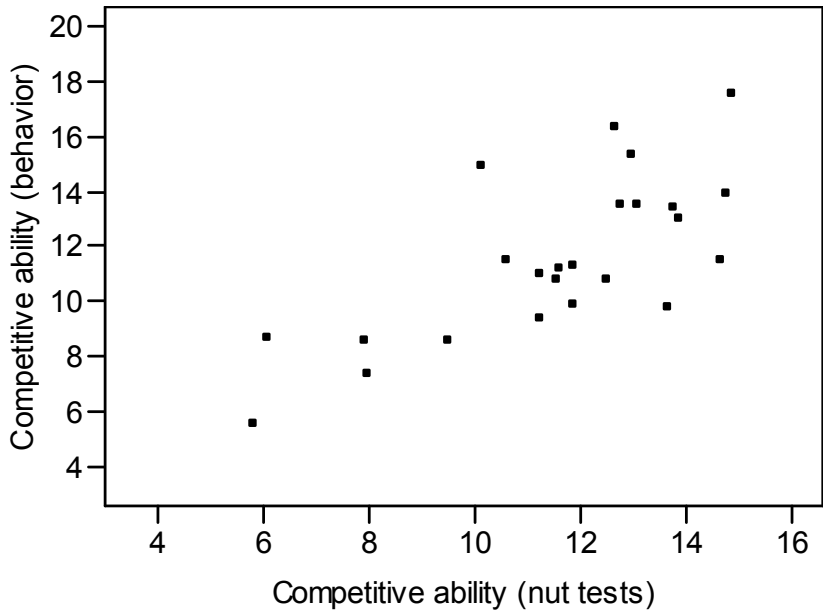


Figure 2-4 Correlation between the competitive ability scores derived from the nut tests and from naturally occurring agonistic interactions.

Discussion

In this study, we validated the normalized David's score (David 1987; de Vries et al. 2006) as a cardinal measure of male competitive ability in a group of Barbary macaques. To derive individual competitive ability scores, we used a semi-experimental method where the males competed among themselves in order to get access to a prized food resource. Syme (1974) pointed out that a competitive ability measure must be internally valid so that it does not merely reflect the capacity of animals to perform in an experimental task. This requirement was clearly fulfilled, since no specific skills were required to obtain the peanut (e.g. no apparatus was involved). Moreover, we reasoned that if the outcomes of the peanut tests were to truly reflect male competitive ability, these should not be influenced by confounding factors such as the respect of ownership, social tolerance or the motivation to win (cf. de Waal, 1989). We designed the semi-experimental protocol in a way that we could control for the first two factors (see Introduction), and we could exclude an influence of motivation since males almost always showed a positive response in specific and general motivation tests. This result is not surprising giving that the incentive used was a peanut, which is a prized food item with high energy content.

The precision of estimates of the competitiveness of males might have been affected by an additional confound not considered in this study, namely the inhibition to contest due to the presence of third parties. The influence of bystanders on the outcome of competitive encounters was demonstrated a long time ago by Kawai (1958), who observed that the mere presence of the mother could influence the outcome of sweet potato tests among juvenile Japanese macaques. Among adult Barbary macaques, Kuester & Paul (1992) reported that prime males which were the target of regular coalitionary aggression by older, subordinate males, could only benefit from their superior physical condition in a competitive situation if a post-prime male "almost surely" received no aid. Thus, it is possible that prime males were less inclined to exert their priority of access when tested against a weaker post-prime male if this latter had a potential coalition partner at hand, i.e. if another post-prime male was a bystander. However, the observation that prime males showed among the highest competitive ability scores (see above) suggests that the effect of by-standers on the estimation of competitive ability scores was negligible. In any case, the proposed protocol may be useful to field biologists interested in investigating the influence of by-standers on the outcome of encounters in organisms that frequently rely on third-parties to resolve their conflicts (reviewed in Harcourt and de Waal, 1992).

We expected that a measure of competitive ability exempt of the influences mentioned above would correlate with some intrinsic features of males. Our results suggest that male age is a good predictor of competitive ability in Barbary macaques, as this factor alone could explain 64% of the variability observed. The relationship between competitive ability and age is likely to have been mediated by male physical condition, because body size, body weight and canine size also appears to follow a bell-shaped relationship with age in Barbary macaque males and other primate males (e.g. de Turckheim and Merz, 1984; Noë and Sluijter, 1995; Setchell et al., 2006) or other polygynous mammals (e.g. Clutton-Brock et al., 1979). In the study group, it is noteworthy that all the 10 "athletic" prime and early post-prime males that still had intact canines showed among the highest competitive ability scores (mean: 13, range: 10.12 – 14.83). A positive relationship between male ordinal rank and physical condition, with prime adult males occupying top positions, was also found in other macaques and baboons (Macaca fascicularis, van Noordwijk and van Schaik, 1985; 1987; M. thibetana, Deng and Zhao, 1987; M. fuscata, Sprague, 1992; Papio anubis, Bercovitch, 1988). The proposed cardinal score may be useful in future studies aiming at examining the relationship between competitive ability and multiple male traits in primates and other animals (for an alternative see Stuart-Fox et al., 2006). Physical characteristics are relatively easy to measure in captive groups and it might be possible to design some simple experiments to determine for example, the maximum amount of weight an individual can lift up (for a measure of total strength in humans see Gurven et al. 2006). However, it would be more difficult to estimate non-physical traits such as personality traits or tactical skills which may also affect competitive ability in organisms like primates (e.g. Goodall, 1986; Sapolsky and Ray, 1989).

In sum, we think that internal validity was achieved and believe that the proposed score is likely to be a reliable estimate of male competitive ability in the study group. The fact that the competitive ability scores derived from the peanut test matrix and those derived from the behavioral matrix were highly correlated in the study group, suggests that both methods might be used as alternatives in Barbary macaques. If such a finding is replicated in studies of other species, it would permit the conclusion that observations of spontaneous interactions suffice to estimate the distribution of competitive abilities of individuals.

Does competitive ability equate RHP?

Parker (1974) coined the term RHP (resource holding potential), which he defined as a "measure of the absolute fighting ability of a given individual" (p. 225), or the ability of an animal to win an escalated fight if one were to take place. RHP has been a challenging concept to measure and behavioral biologists commonly rely on correlates of RHP in studies of aggression in animals (e.g. Haley, 1994; Sneddon et al., 1997; Gherardi, 2006) rather than direct measures of it. In primates, it is generally assumed that male RHP is partially reflected by his place in a linear rank order, but the difference in fighting ability between two males is also important (Noë, 1994).

The measure of competitive ability proposed in this paper may thus be preferred to ordinal ranking as an estimate of RHP in primate males and similar organisms.

However, two important limitations should be pointed out. First, naturally occurring fights in group-living species such as primates are usually rare because individuals repeatedly meet with each other (i.e. they are familiar) and use signaling to avoid escalated aggression, including the establishment of dominance relationships (Preuschoft and van Schaik, 2000). Thus, in animals that characteristically have formalized dominance relationships and strictly linear hierarchies, dominants will always induce submission in lower-ranked individuals, and the difference in normalized David scores between any two adjacent ranking individuals will be identical, regardless of the actual differences in RHP among the animals (i.e. the cardinal measure behave as an ordinal measure, see Fig. 2-1). However, this problem is less pronounced in species such as Barbary macaques where male relationships are less clear-cut and the weaker male of a dyad sometimes wins the encounter (e.g. Kuester & Paul 1992; Brauch et al. 2008; this study, Table 2-1). In this case, the proposed cardinal measure would provide a closer estimate of a male's relative RHP than an ordinal measure of competitive ability.

Second, Parker (1974) originally conceptualized RHP as an absolute measure of an individual's fighting ability. Yet, competitive ability (or fighting ability) can only be inferred from the actual outcome of dyadic encounters (win, draw or loss), because there is no independent and absolute yardstick to rate the animals' competitive ability. At best, an animal that wins a contest can be assumed to have performed at a higher level than his opponent for that contest. The inevitable conclusion is that any system aimed at rating the individuals based on the outcome of encounters produces a *relative* measure, dependent on the given assemblage of males present. However, this should not constitute a real problem, as long as direct comparisons in RHP measures between individuals living in different groups are not required. Despite the drawbacks mentioned above, the relative estimate of male competitive ability proposed in this paper was successfully used to test an assumption used in several models of coalition formation in animals (e.g. Noë 1994, Pandit & van Schaik 2003, van Schaik *et al.* 2004, 2005, Whitehead & Connor 2005) that a coalition would be successful if the sum of the competitive abilities (or fighting abilities) of the coalition partners is more than the competitive ability of their target (Chapter 3).

Chapter 3

Coalitions in male Barbary macaques: strength, success and rules of thumb

Several quantitative models of coalition formation assume that a coalition is successful if the strength of the coalition is greater than the strength of the target, but unsuccessful otherwise. However, strong empirical evidence in favor of this hypothesis is still lacking. In this study, we provide an empirical test of this assumption in Barbary macaque males, by using a field-based estimate of individual competitive ability from which coalition strength is derived. Coalition success was determined for 90 coalitions composed of two partners and targeted at one male. Of these 72.2% were behaviorally successful and 27.8% were unsuccessful. Asymmetry in strength was a significant predictor of coalition success, as this factor alone could explain up to 78.6% of coalition outcomes in the study group. Males behaved as if they were at least partially informed about the nature of this asymmetry. The targets of coalitionary attacks were more likely to counter-attack as asymmetry in strength decreased, and coalition partners formed coalitions that produced on average a greater asymmetry in strength than would be expected by chance. However, we provide evidence that males may have used simple rules of thumb based on their knowledge of dyadic and third-party relationships, rather than estimates of asymmetry in strength per se. We conclude that competitive ability is an important factor in coalition formation in Barbary macaque males and discuss additional factors not included in this study, which may account for the unexplained outcomes.

Bissonnette A., de Vries H., van Schaik C.P. Animal Behaviour (in press)

Introduction

Parker (1974)coined the term RHP (resource holding potential), which he defined as a "measure of the absolute fighting ability of a given individual" (p. 225), or the ability of an animal to win an escalated fight if one were to take place. Ample evidence exists that correlates of fighting ability such as body weight, body size, weaponry, etc. are important in deciding dyadic outcomes in animals (Arnott and Elwood, 2009). In contrast, the importance of fighting ability in polyadic conflicts involving for example, two coalition partners and one target, has received less attention. Much theory on coalition formation in animals is built on the assumption that a coalition would be feasible and thus successful if the strength of the coalition (i.e. the sum of the fighting abilities of the coalition partners) is more than the strength of their target (e.g. Noë 1994, Pandit & van Schaik 2003, van Schaik *et al.* 2004, 2006, Whitehead & Connor 2005), and there is some indirect empirical evidence supporting that assumption in primate males (Bercovitch, 1988; Noë and Sluijter, 1990, 1995; Silk, 1992a). For example, Noë (1994) developed a post-hoc descriptive model of coalition formation in savanna baboon males with fighting ability as a central parameter to explain the observation that only a subset of males that occupy middle or lower ranks frequently form coalitions, while the highest and lowest ranking males are little involved in coalition formation (reviewed in Noë, 1992, table 11.1). Male fighting ability was not measured directly but modeled using a set of reasonable assumptions, so that males could be assigned to a fighting ability slot according to their ordinal rank order. The main conclusion was that males of intermediate fighting ability are more likely to be seen in coalitions since the number of potentially successful partner-target combinations is highest for those males.

A major impediment for detailed empirical investigation of the role of fighting ability in coalitionary contests is the lack of a quantitative measure of fighting ability that would allow the assessment of the *combined* fighting ability of the coalition partners (or coalition strength) in relation to their target. The use of correlates of fighting ability, such as body weight, body size, weaponry, etc., to predict coalition outcome is problematic, if only because fighting ability in organisms like primates are likely to be determined by a combination of these factors, and it is unclear how these factors would sum up to give coalition strength. Recently, Bissonnette et al. (Chapter 2) validated a quantitative estimate of male competitive ability based on the outcome of dyadic competitive encounters in a group of Barbary macaques. Competitive ability was defined as the "ability of an animal to claim a resource by means of force or the threat of force" (cf. de Waal, 1989, p. 246), and was estimated in a semi-experimental setting. The authors concluded that despite its limitation, this measure is often preferred to ordinal ranking as an estimate of RHP as defined by Parker (see above).

Here, we use this competitive ability score to derive coalition strength, and test the correctness of the assumption of several quantitative models of coalition formation that a coalition is successful if the strength of the coalition is greater than the strength of the target (e.g. Noë, 1994; Pandit and van Schaik, 2003; van Schaik et al., 2004; Whitehead and Connor, 2005). The working hypothesis was formulated as follows: Coalitions are more successful as the asymmetry between the strength of the coalition and the strength of the target increases, i.e. as ($S_{partner1}$ + $S_{partner2}$) - S_{target} becomes larger. We refer to this difference as 'asymmetry in strength'. The working hypothesis was tested against the null hypothesis that competitive ability is irrelevant and two males can always beat one.

As mathematical models should not be confused with the way animals make behavioral decisions (Marsh, 2002), our second objective was to assess whether male coalitional decision-making is also based on asymmetry in strength. A number of observational and experimental studies have shown that primates living in stable associations (including macaques) have knowledge of direct dominance relationships (i.e. stronger or weaker than self) and third-party dominance relationships (Fig 3-1), and that this knowledge is used by monkeys to recruit coalition partners in 'bridging' and 'all-down' coalitions (Perry et al., 2004; Silk, 1999). 'All-down' coalitions occur when both coalition partners are stronger than the target, while 'bridging' coalitions are instances where one partner is stronger and one weaker than the target (van Schaik et al., 2004; cf. Chapais, 1995). Barbary macaque males often form all-up coalitions, where two weaker males attack a stronger target (Kuester & Paul 1992; this study, Chapter 4). In this coalition configuration, males would need additional information about relative coalition strength to assess whether two weaker males together are strong enough to beat a stronger target (Fig. 3-1).

We investigated this issue by looking at the behavior of the target in the early phase of the coalitionary conflict. Assuming that males have perfect information about the asymmetry in strength, we would expect the target to be more likely to counter-attack as the asymmetry in strength decreases. We then assessed whether males form coalitions that produce on average greater asymmetry in strength than would be expected by chance alone. This would indicate that coalition partners consider somehow their probability of winning when deciding to form a coalition, as a larger asymmetry in strength is expected to be associated with a higher probability of success.

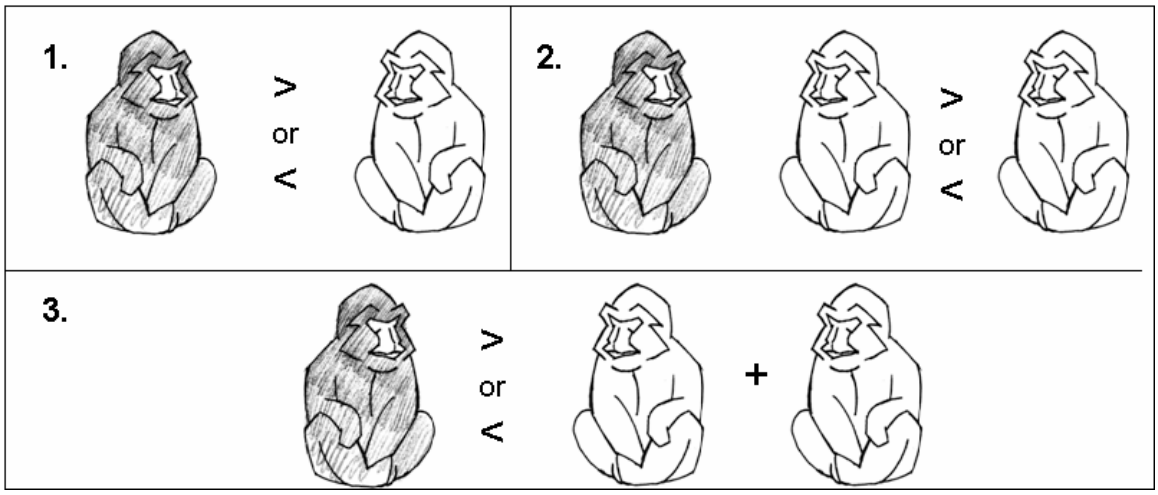


Figure 3-1 What monkeys living in stable associations know about relative strength. There is evidence suggesting that Ego (in grey) has knowledge of: (1) direct relative strength and (2) relative strength of others, and can use this information to draw inferences about the relative strength of all-down and bridging coalitions, but to date there is no evidence suggesting that Ego has knowledge of the relative strength of two weaker individuals together (3).

Methods

Study species and coalition formation

Barbary macaques live in multi-male multi-female groups. They are seasonal breeders (e.g. de Turckheim and Merz, 1984; Fa, 1986) and have a mating season ranging from early August to late March, with a peak in mating activities in November and December (Kuester and Paul, 1984). Coalitions in Barbary macaques are the almost exclusive domain of post-prime males and mostly target stronger, prime adult males (Kuester and Paul 1992; this study). Coalitions are most frequent during the mating season (A. Paul, pers. comm.) and can be an efficient mating strategy enabling individually weaker males to increase their access to attractive females (Kuester and Paul, 1992), although most coalitions occur in the absence of resources (Chapter 4).

In this paper, a coalition is defined as simultaneous aggression directed by two partners against a common target (cf. de Waal and Harcourt, 1992). We included both *parallel coalitions* where two males simultaneously initiate an aggression against a common target (e.g. savanna baboons: Noë, 1986), and *interference coalitions* where one male intervenes in an on-going conflict and sides with one of the two opponents (e.g. bonnet macaques: Silk, 1992b; Tibetan macaques: Berman et al., 2007; cf. Noë, 1994). Aggressive acts shown by the coalition partners included displacing, lunging at, grabbing, slapping and chasing (see Appendix B for behavioral definitions).

Study site and animals

The study was conducted during the mating season 2006-2007 (September to mid-February) at the Affenberg Salem, Germany, where three groups of Barbary macaques live throughout the year in a 14.5-ha mixed beech-spruce forest, bushes and open meadow (for a complete history of the colony see de Turckheim and Merz, 1984; Paul and Kuester, 1988). The monkeys are provided once daily with widely dispersed fruits, vegetables and grains and also feed routinely on natural vegetation. Water and monkey pellets are available *ad libitum*. The data were collected on one group (H), which was composed of 27 adult females (> 5 years old), 7 prime males (aged between 7 and 12 years old), 17 post-prime males (≥ 14 years old) and 6 juveniles. All adult animals were recognized individually and habituated to the observers.

Behavioral observations

A total of 279 hours of male focal data (Altmann, 1974) was collected by A.B., whereby detailed information on coalitionary interactions among adult males was recorded. The coalition data base was supplemented by *ad libitum* data (Altmann, 1974) which were recorded by A.B. and two additional observers (Elena Lange and Nicole Bischofberger) throughout the day. Data on coalitions included among other things: (1) the date and time of the interaction, (2) the identity of the coalition partners and their target, and (3) the behavior of the contestants. Of the coalitions that are used in this paper, 56.8% were collected by A.B. The inter-observer consistency could not be systematically tested because of the rapidity and unpredictability of coalition formation, but a good qualitative agreement was found among the three observers for the few coalitions that were observed simultaneously. The percentage of agreement (cf. Martin and Bateson, 2000) for focal sampling between A.B. and N.B., and A.B. and E.L., reached at least 80%.

Estimating competitive ability

The method used to estimate individual competitive ability is described in Chapter 2. Briefly, the competitive ability scores are based on peanut tests which were performed opportunistically by E. L. and A.B during the same period when the coalition data were collected. Each test consisted of throwing a nut between two adult males (hereafter rivals). This protocol was used because it allowed the exclusion of three factors other than competitive ability (i.e. respect of ownership, social tolerance and motivation) that may influence the outcome of dyadic encounters in group-living primates (de Waal, 1989). According to their outcomes, the tests were classified into two mutually exclusive categories: a test was either (1) ‘decided’ when one rival ate the nut or (2)’tied’ when neither of them ate the nut. Individual competitive ability was calculated using the normalized David’s score (David, 1987; de Vries et al.,

2006). The David's score provides a cardinal score for each animal based on the outcome of dyadic encounters with other group members, while taking the relative strength of their opponents into account. This score is considered to be a valid measure of individual success in Barbary macaques (Chapter 2) and other animals (Gammell et al., 2003; Hemelrijk et al., 2005; de Vries, 2009). It is important to stress that this system, and any other system that aims at rating the individuals based on the outcome of encounters, produces *relative* scores, which implies that the scores depend on the assemblage of males present in the group. This is not an issue here, as the peanut tests and the coalition data were collected in the same group-period.

Success of coalitions

The success of a coalition was evaluated from the behavior of the coalition partners and the target at the termination of the conflict. A coalition was considered to be (1) *successful* when the target immediately showed submissive behavior (i.e. walked away, fled, climbed a tree) without counter-attacking or counter-attacked but showed submissive behavior in direct response to aggression from the coalition partners at the end of the conflict; and (2) *unsuccessful* when the coalition partners showed submissive behavior at the end of the conflict in response to counter-attack from the target.

Statistics

Logistic regression (Quinn and Keough, 2002) was used to determine the significance of the independent variable "asymmetry in strength" and to determine the percent of variance in the outcome variable "success of coalitions" explained by the independent variable. The variable "success of coalitions" was determined as explained above (coded 1 if behaviorally successful and 0 if unsuccessful). The fixed factor "asymmetry in strength" was calculated as the sum of the strengths (or competitive abilities) of the coalition partners minus the strength of the target that is, $S_1 + S_2 - S_t$. This variable is continuous and increases as the strength of the coalition partners increases and/or the strength of the target decreases. Random effects were included in the model to control for non-independence at the individual and the coalitional level (i.e. each individual contributed differentially to the outcome of the coalition across different events and a particular coalition may have been particularly successful or not because of its composition). For each individual we created a new binary variable indicating whether the individual was one of the partners in the coalition (indicated by a 1) or not (indicated by a 0). The set of random effects includes the variable Target and these 20 binary individual variables. So, for each observation the two 1's indicate which two animals were partners in the coalition.

We used the Wald statistic to test whether the independent variable has a statistically significant relationship with the outcome variable. This statistic corresponds to significance testing of *b* coefficients in ordinary least square regression

and can be compared to the standard normal (z) distribution (Quinn and Keough, 2002). All analyses were performed using the library lme4 of the program R v. 2.6.0 (The R Foundation for Statistical Computing, Vienna, Austria). The significance level alpha was set to 0.05.

The percentage of variance in the outcome variable explained by null hypothesis H_0 (i.e. all coalitions are successful) was directly calculated from the observed data. The percent of variance in the outcome variable explained by the independent variable specified under the hypothesis H_1 (asymmetry in strength) was calculated from the fitted logistic regression model. Because the logistic regression equation, which is a linear equation, does not predict the binary variable itself, we had to choose a cut-off value below which 0 (unsuccessful) and above which 1 (successful) is predicted. A variety of approaches are possible to determine where this cut-off point is to be located (Neter et al., 1996). Here, we found the best cut-off for the data set by selecting by trial-and-error the probability value that results in a balance between the proportion of 'successful' and 'unsuccessful' coalitions correctly predicted (Scott et al., 2002).

We conducted a Monte-Carlo simulation to determine the likelihood that the observed mean value of asymmetry in strength or a greater value could occur by chance. In this simulation, a combination of two partners and one target was chosen at random from a pool constituted of all males that were seen at least once in an all-up coalition (N=15) and all males that were targeted at least once by an all-up coalition (N =7). The asymmetry in strength was calculated for every partners-target combination. Each run was constituted of 52 randomly chosen combinations, which corresponds to the number of all-up coalitions included in the analysis. The mean asymmetry in strength of the 52 chosen combinations was then recorded for each run. 10 000 runs were performed to generate a distribution of values. The observed value (i.e. the mean asymmetry in strength calculated from the observed cases) was compared against the results of the simulation to examine the likelihood that the observed value or a greater value could occur by chance. The p-value was calculated as the proportion of sampled runs where the mean asymmetry in strength was greater than or equal to the observed value. Programs for the simulation were written in Perl (Wall et al., 2000).

Results

A total of 111 male-male coalitions were documented during the study period. A subset of 21 coalitions was excluded from this study, either because the identity of one participant was unknown (two cases), the behavior record of the participants was not sufficiently detailed (12 cases), or a female (with undetermined strength) joined the coalition (two cases). Coalitions involving three males (three confirmed and two possible cases) were also excluded. Coalition success was unambiguously determined

for the 90 remaining coalitions. All 90 coalitions were composed of two partners and targeted at one male.

Effect of competitive ability on coalition success

The null hypothesis (H_0) states that competitive ability is irrelevant and that coalitions are always successful. According to the criteria described in the Methods, 72.2% (65/90) of the coalitions were behaviorally successful and 27.8% (25/90) were unsuccessful. This means that the null hypothesis correctly explains 100% of the successful coalitions and 0 % of the unsuccessful ones, for an overall fit of 72.2%.

The alternative hypothesis (H_1) states that competitive ability is relevant and coalitions are more successful as the asymmetry between the strength of the coalition and the strength of the target increases. Regression analysis shows that asymmetry in strength is a significant predictor of coalition success in the study group (Wald test: $z= 4.01$, $P<0.0001$). This hypothesis provides a better fit than the null hypothesis. It correctly explains 60% (15/25) of the successful coalitions and 86.2% (56/65) of the unsuccessful ones, for an overall fit of 78.6%.

The fitted logistic curve is depicted in Fig. 3-2a. We can see that the probability of coalition success increases with the asymmetry in strength, as expected. The cut-off value for which the proportion of incorrect predictions of unsuccessful and successful outcomes was lowest corresponds to an asymmetry in strength of +5.23 (i.e. a coalition is predicted to be successful when the asymmetry in strength is greater than 5.23 and unsuccessful when 5.23 or less).

A test-case: all-up coalitions

Coalitions can occur in three different configurations according to the competitive ability of the coalition partners relative to their target (see Introduction). In all-down and bridging coalitions, at least one partner is individually strong enough to beat the target. As expected, all-down (N=8) and bridging coalitions (N=29) were almost always successful (success all-down: 100%; bridging: 82.8%). All-up coalitions allow us to evaluate the extent to which the *combined* competitive abilities of the partners determine the outcome of coalitions, and as such constitute a test-case. Of the all-up coalitions 59.6% (31/52) were behaviorally successful and 40.3% (21/52) were unsuccessful. We repeated the analyses with the data set comprising only the 52 all-up coalitions. The probability that a coalition wins still increases significantly with asymmetry in strength (Wald test: $z= 2.80$, P=0.005). This hypothesis provides an overall fit of 71.2% (67.7% successful, 76.2% unsuccessful), which is better than the 59.6% under the null hypothesis. The fitted logistic curve is depicted on Fig 3-2b. The cut-off value for which the proportion of incorrect predictions of unsuccessful and successful outcomes was lowest corresponded to an asymmetry in strength of 7.37.

Do males have some information about the relative strength of the coalition?

To assess the rules used by males to make decisions concerning coalitions, we first took the point of view of the target and looked at its behavioral response following a coalitionary attack. A detailed account of the behavior of the target in the early phase of the conflict was available for 79 coalitions. Typically, the target's first response was to retreat immediately when attacked by a coalition, but it could decide in the following seconds to counter-attack or not. The targets counter-attacked at least once (including threatening and physical aggression) in 49.4% (39/79) of the coalitions. Univariate logistic regression revealed a significant, negative relationship between asymmetry in strength and the target's response, indicating that targets are more likely to counter-attack as the asymmetry in strength decreases (Wald test: $z = -3.620$, $P = 0.0003$). This simple model (cut-off value: 9.25) correctly explained 69.6% of the cases.

Another possibility would be that targets of coalitions adjust their behavioral response according to the number of stronger opponents. This would not require the target to be able to assess asymmetry in strength *per se*, but only to determine in a dyadic fashion whether the first and the second coalition partners are stronger or weaker than himself. Targets counter-attacked in 72.7% (32/44) of the cases when confronted with an all-up coalition, did so 32.1% (9/28) of the time against bridging coalitions and never counter-attacked (0/7) when confronted with an all-down coalition. Thus, 32 plus 19 plus seven of the 79 cases (i.e. 73.4%) can be explained by the simple rule of thumb: 'do not counter-attack if at least one partner is stronger than yourself and counter-attack otherwise'. This heuristic accounts for a larger proportion of the observed cases than the estimation of asymmetry in strength.

We then took the point of view of the coalition partners and asked whether they form partners-target combinations that have on average a greater asymmetry in strength than would be expected by chance. We conducted a Monte-Carlo simulation to determine the likelihood that the mean value of asymmetry in strength observed occurred by chance. Because all-up coalitions constitute the only appropriate test-case for this question, we focused on this coalition type. The results indicate that the observed value (6.77) was significantly higher than expected if males formed combinations at random with respect to asymmetry in strength (Exact test: $P = 0.0015$, Fig. 3-3). This suggests that coalition partners rely on some estimates of asymmetry in strength when deciding to form a coalition, although the exact means by which this assessment is made remains unknown. This issue is discussed below.

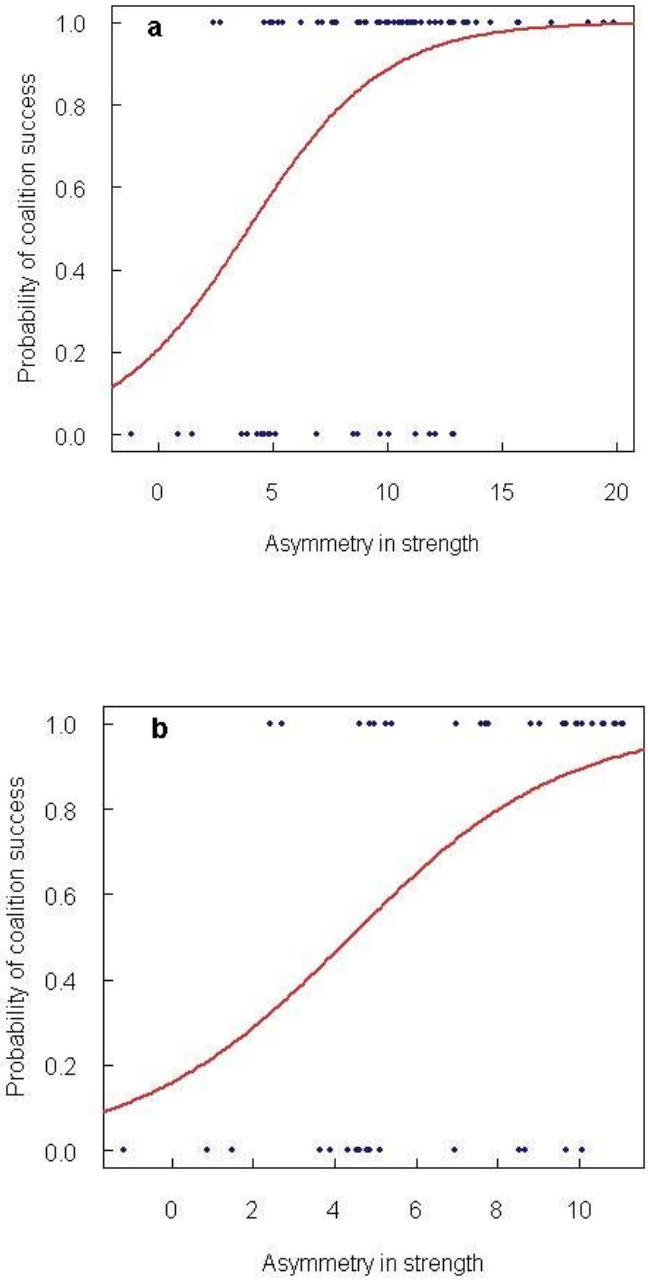


Figure 3-2 Scatter plot of the success of coalitions (1=successful, 0= unsuccessful) in relation to the asymmetry in strength between the coalition and the target for (a) all coalitions (fitted logistic curve: y=-1.35 + 0.39x, N=90) and (b) all-up coalitions only (y=-3.34 + 0.45x, *N*=52).

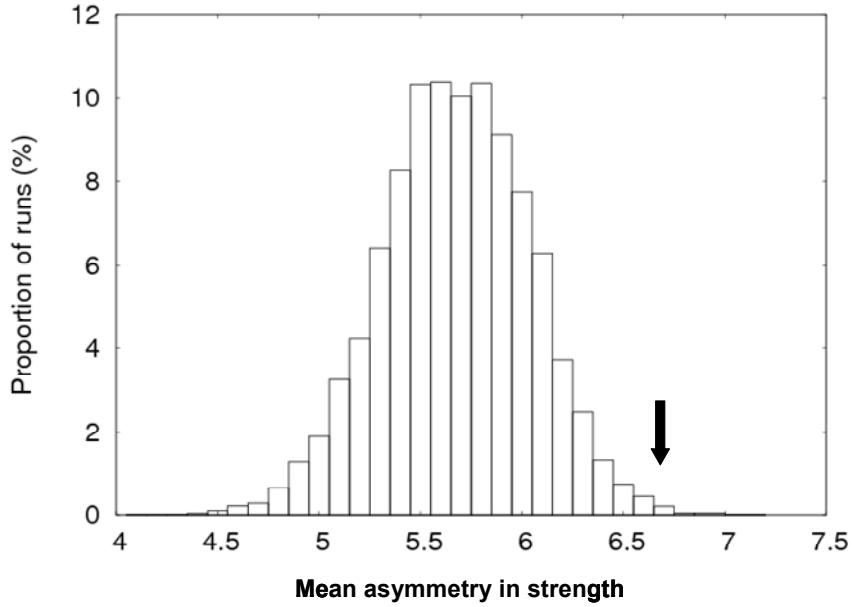


Figure 3-3 Result of the Monte Carlo simulation. In this simulation, a combination of two partners and one target was chosen at random from a pool constituted of all males that participated as target or partner in all-up coalitions. The asymmetry in strength was calculated for each partners-target combination. Each run was constituted of 52 randomly chosen combinations, which corresponds to the observed number of all-up coalitions. The distribution of values is based on 10 000 runs. The observed value, 6.77 (indicated by the arrow) was significantly higher than expected if males formed combinations at random with respect to asymmetry in strength.

Discussion

Several models of coalition formation (references in Introduction) assume that each coalition partner makes a separate and additive contribution to the strength of a coalition, and that a coalition is successful when the strength of the coalition is greater than that of the target. In this paper, we have presented empirical evidence supporting this assumption. The strength of the coalition was calculated from a field-based estimate of individual competitive ability that we introduced in Bissonnette et al. (Chapter 2). We could show that the asymmetry in strength between the coalition and the target was a significant predictor of coalition success, and that this factor alone could explain up to 77.8% of male-male coalition outcomes in the study group. The asymmetry in strength could explain a larger proportion of the variance in the data than the null hypothesis that two males always beat one, and accounted for a substantial proportion of the unsuccessful coalition outcomes (i.e. up to 70%). From a theoretical point of view it would be expected that if competitive ability is important in deciding dyadic outcomes in animals (reviewed in Huntingford and Turner, 1987; Archer, 1988; Arnott and Elwood, 2009), the same would also be true for coalitionary outcomes. This is what our data suggest. However, our results also indicate that the inclusion of a correction factor in the competitive ability formula might be necessary,

so that a coalition is successful when the asymmetry in strength is greater than zero and unsuccessful otherwise (i.e. $S_{partner1} + S_{partner2} - S_{target}$ – correction factor, see Fig. 3-2). This may suggest that our measure of competitive ability is not completely accurate (see below), or that there are inherent, fixed costs to coalition formation so that a coalition never reaches its full potential. Such costs would arise, for example, if males constantly need to monitor the actions of their partner ('Would the partner defect of not'?) and as a result can never fully take part in the interaction. It is too early to draw any firm conclusions and this issue will wait further investigation. Overall, our findings are in line with previous studies in baboons and macaques, which presented evidence that competitive ability (estimated from rank) is an important factor in coalition formation among males (Bercovitch, 1988; Noë, 1989; Silk, 1992a; Noë and Sluijter, 1995).

About 22% of all coalition outcomes could not be explained by the asymmetry in strength. Several technical and biological reasons may contribute to explain the lack of perfect fit, but we restrict the discussion to the most important ones. First, it is possible that asymmetry in strength is the primary factor in coalition success, but our estimate of competitive ability and thus coalition strength is not completely accurate. The estimate of competitive ability proposed by Bissonnette et al. (Chapter 2) relies on the assumption that the ratio of wins and loses between individuals of a given group is proportional to their relative competitive ability. However, in group-living species such as primates, individuals are usually familiar and avoid escalated aggression by establishing dominance relationships (Preuschoft and van Schaik, 2000). Initially, relative competitive ability among males determines their relative rank, but when dominance relationships are established dominants will generally induce submission in lower-ranked individuals. Thus, in the extreme case of a strictly linear dominance hierarchy where all dyadic encounters are won by the dominant individual of the pair, the difference in competitive ability between any two adjacent ranking individuals will be identical, regardless of their actual differences in competitive ability (e.g. the ratio of wins and losses is always one). This problem is less pronounced in Barbary macaques where male dominance relationships are not strictly linear and the weaker male of a dyad sometimes wins the encounter (e.g. Kuester and Paul 1992; Brauch et al. 2008; this study), but we cannot exclude the possibility that the asymmetry in strength between the coalition partners and the target may have been overestimated or underestimated to a certain extent. Any method that aims at estimating male competitive ability from dyadic encounters among familiar animals will show the above described limitation, but because competitive ability can only be measured in relation to others, it is unclear how that problem can be solved.

Second, it is possible that in addition to asymmetry in strength, other factors might have influenced the outcome of coalitionary conflicts. A number of empirical studies have confirmed that the probability of victory for a weaker animal increases when its resource value or level of motivation increases (e.g. Popp, 1987; Lemel and Wallin, 1993; reviewed in Enquist and Leimar, 1987). Consequently, it appears reasonable to consider the possibility that motivation might also affect the outcome of

coalitionary conflicts. For example, we have observed one interesting case where a target defeated two coalitions in a row, while the asymmetry in strength would have predicted the defeat of the target in both cases. Thus, a coalition that is strong enough to beat its target might sometimes be unsuccessful if the motivation of the target was higher than that of the partners, and vice-versa. How to estimate motivation is an important empirical question that needs to be addressed in future work.

Third, Noë (1994) suggested that the effective strength of a coalition may be affected by its level of coordination, so that two individuals attacking in a very coordinated manner would be more effective than a coalition where one partner 'does not pull his weight'. It has been reported that 'successful coalitionary challenges [in baboon males] rely on tightly orchestrated, (coordinated) movements among allies' (Smuts, 1985, p. 145), although it remains unclear how a well-structured coalition should be choreographed. Is a coalition well-coordinated when the partners perform similar actions in time and space (Fig. 3-4), or when the partners perform different complementary actions towards the same target, for example by attacking from different directions? Complementary actions by the coalition partners towards the same target appear to be very rare or even absent in Barbary macaques (own obs.), but this issue needs to be investigated in more details. The importance of communication in promoting coordination among the coalition partners (Noë, 2006) is another issue that needs to be addressed in future work.

Figure 3-4 A coalition in Barbary macaque males. The two coalition partners (on the right side) stand in parallel in body contact while challenging their target.

Is asymmetry in strength represented in the decision making process of males?

To make advantageous decisions about when and with whom to form a coalition, and whether or not to counter-attack in the early phase of the conflict when being the target of a coalitionary attack, Barbary macaque males would benefit from being able to assess the relative strength of the coalition. In this study, males behaved as if they were at least partially informed about the nature of this asymmetry. Indeed, we have provided evidence that targets of coalitionary attacks were more likely to counter-attack as asymmetry in strength decreased, and coalition partners formed coalitions that produced on average a greater asymmetry in strength than would be expected by chance. The possibility that males can somehow compute relative coalition strength from the individuals comprising is unlikely, because this would represent a cognitively challenging task for macaques (and humans alike). Thus, by what means do males assess relative coalition strength?

In primates living in stable associations, an individual accumulates information about direct relative strength and third-party relative strength (Fig. 3-1) through repeated competitive interactions in which it is directly involved, and by 'eavesdropping' that is, by watching interactions in which it is not directly participating (Tomasello and Call, 1997; Preuschoft and van Schaik, 2000). The same could be true for relative coalition strength (Fig. 3-1), but we think that this is unlikely in the present case for the following reasons. First, coalitions were mostly formed opportunistically by different combinations of males, with very few dyads and triads having been observed more than once during our sampling (own obs.), allowing only limited room for some form of associative learning of successful partner-target combinations. Second, we found no evidence that the success of coalitions increases as the mating season progresses, which would have suggested that some kind of learning by the coalition partners is involved (coalition success, October: 66.6%, November: 84.2%, December: 42.9%, January: 58.3%). Third, the opportunities of eavesdropping were apparently limited, as coalitions often occurred in the absence of by-standers (own obs.).

We suggest that coalition partners and targets alike may have relied on simple rules of thumb based on their knowledge of dyadic and third-party relationships. Indeed, we found evidence suggesting that the targets of coalitions decided to counter-attack based on a simple heuristic: are none, one or both of the allies outranking him (Fig. 3-5)? The number of stronger opponents is readily available information which allows a rapid categorization and provides a fairly good (but nevertheless imprecise) approximation of relative coalition strength. Partners of all-up coalitions may have also relied on a simple rule of thumb, such as: choose the strongest partner at hand. The systematic use of this heuristic would have led to coalitions that are on average stronger than coalitions formed at random, which would account for the finding that males are more likely to form partners-target combinations with a greater asymmetry in strength. Unfortunately, this hypothesis could not be formally tested in this study. To do so, one would need to look at the

patterns of recruitment and determine which male is usually solicited among the potential candidates present (Silk, 1999; Perry et al., 2004), but data were not available for a sufficient number of coalitionary attacks. An alternative would be for males to choose the cheapest winning coalition, especially in cases where the interests of the partners overlap, for example when a coalition serve to get access to an estrous female, which cannot be shared (Gamson, 1961; Noë, 1989). However, this alternative is unlikely, as this would require males to be able to estimate the asymmetry in strength. Overall, these findings are in line with a body of research that has demonstrated that humans and non-human animals use heuristics to make complex decisions when faced with constraints in time, energy, and computational capacity (Hutchinson and Gigerenzer, 2005).

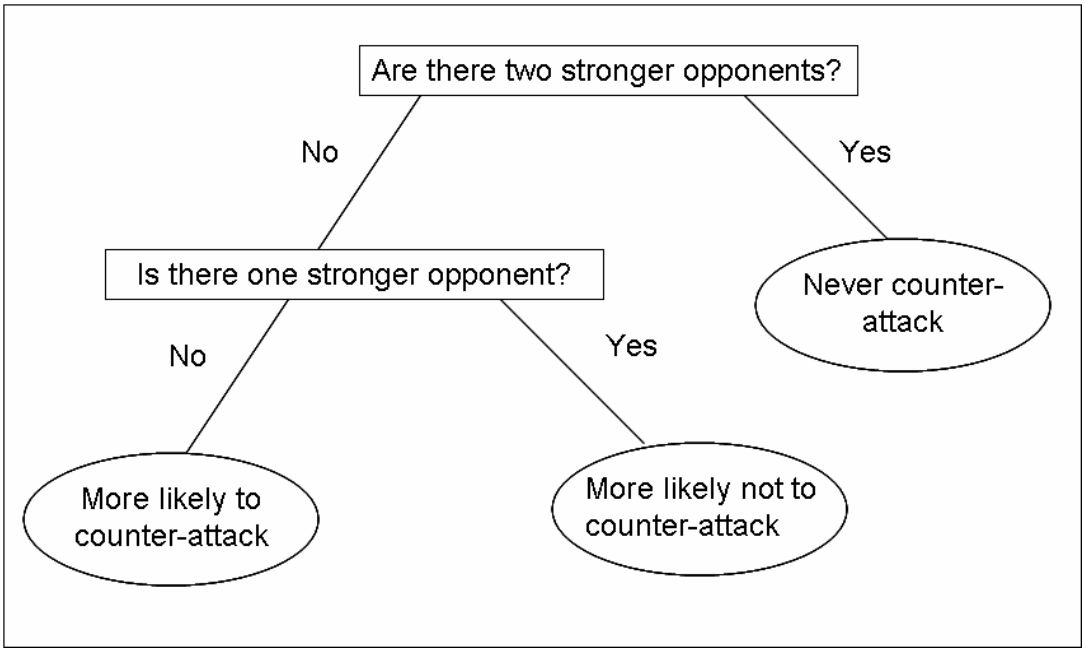


Figure 3-5 A simple decision tree reflecting the target's decision to counter-attack or not in the early phase of the conflict.

Chapter 4

Leveling coalitions by male Barbary macaques

According to current socioecological theory male-male cooperation is expected to be unusual among group-living primates, largely because the resource males compete for (i.e. fertilizations) is not shareable. Nevertheless, primate males are known to use coalitions in different ways to improve their mating success, although detailed accounts of naturally occurring coalitions remain scarce. In this study, we examine the patterning and function of coalitions among males in two semi-free ranging groups of Barbary macaques in the context of mating competition. Coalitions were frequent in one study group and evidence indicates that coalitions were mostly used by mid-low ranking, post-prime males to level mating access. Coalitions over attractive females represented one-third of all coalitions and produced a successful changeover about half the time. We found evidence that post-prime males may also use coalitions in the absence of any direct competition over females as an offensive tactic to isolate higher-ranking, prime males in the trees during the mating season. Coalitions were very rarely observed in the other study group composed of many adult males but only one post-prime male, which indicates that coalitions in this species are expressed in a strongly age-related fashion. Possible reasons for the age-dependence of coalitions are discussed.

Introduction

Male-male cooperation is expected to be unusual among group-living males, largely because the resource for which males compete for (i.e. fertilizations) is not shareable (van Hooff and van Schaik, 1992; van Schaik, 1996). Nevertheless males of some mammalian species sometimes cooperate to improve their access to fertile females, and one way to do so is by coalition formation. A coalition can be defined as joint aggression between at least two individuals against a common target (de Waal and Harcourt, 1992), often preceded by signaling between the attackers (e.g. "show-looking": de Waal et al., 1976; "head-flagging": Packer, 1977). Primate males can use coalitions in different ways to improve their mating success (Smuts, 1985; van Schaik et al., 2006). They can use coalitions to expel a breeding male from a one-male group and take over the group, or to repel extra-group males (reviewed in Smuts et al., 1987). Within –group coalitions may involve males mounting a coalitionary challenge against a higher-ranker thus leading to an improved rank and consequently improved mating access for one or both coalition partners (reviewed in Smuts et al., 1987). Within-group coalitions may also be formed to improve the partners' access to estrous females without having any permanent effect on the rank of the partners. The best documented cases have been reported in savanna baboon males (reviewed in Noë, 1992), and anecdotal reports exist in one macaque species (e.g. Tonkean macaques, Thierry, in press). We will use the terminology suggested by Pandit and van Schaik (2003) and refer to this last type of within-group coalitions as "all-up, leveling" coalitions.

In technical terms, all-up leveling coalitions are expected to alter the distribution of payoffs (in terms of matings or paternities) among males and make it more egalitarian (cf. Pandit and van Schaik, 2003). In theory, the same leveling coalitions may also be found when no resource is directly at stake (van Schaik et al., 2006). This can occur, for example, if coalitions serve to undercut the intrinsic power of high-ranking males or intimidate them, thus leading high-rankers to show some restraint in mating competition. There is some circumstantial evidence suggesting that this variant of leveling may occur in Barbary macaques. Indeed, it was reported that although coalitions are used by older males as an efficient mating tactic to increase their mating success (Kuester and Paul, 1992; Paul et al., 1993), coalitions are rarely formed to get direct access to estrous females and apparently do not have any permanent effect on the rank of the partners (for one possible example of rank-changing coalition in Barbary macaques see Witt et al., 1981). Instead, it was suggested that coalitions were used by older males during the mating season to drive away more dominant, younger adults, resulting in them being isolated in trees and refraining from competition during the day (Kuester and Paul, 1992; Paul et al., 1993). Because Barbary macaques are mostly terrestrial (Fooden, 2007), it may

indeed be advantageous for older males to isolate rivals in the trees as an offensive tactic to prevent them access to receptive females. However, solid evidence for this "intimidation" hypothesis are still lacking.

The goal of this paper was to provide a first systematic description of the context of occurrence and patterning of male-male coalitions in Barbary macaques. We were especially interested in determining the function(s) of coalitions in this species, and whether coalitions may be used as a mean to intimidate stronger rivals as suggested by previous authors (see references above). The "intimidation" hypothesis predicts that an important part of the coalitions formed during the mating season occur in the absence of any direct competition over females. Most coalitions should be directed up the hierarchy ("all-up"). Because age and rank are related in Barbary macaque males (Kuester and Paul, 1992; Paul, 1989), older (subordinate) males should have most to gain by intimidating younger (more dominant) adults and consequently be more likely to participate in leveling coalitions. The hypothesis further predicts a difference in the spatial locality of the frequent targets of coalitions in comparison to non-targets. If coalitionary threat is highest on the ground (as would be expected following the reports of Bercovitch, 1988; Kuester and Paul, 1992), then targets of coalitions should be more likely to spend time and form their consortships (if any) in the trees.

Methods

Study sites and study groups

Daun group

The first part of the study was conducted by A.B. and Claudiane Beaudoin during the mating season 2005/06 (September to mid-February) in the Wildpark Daun (Eifel, Germany). The colony was established in 1998 with 24 animals from Gibraltar. These animals were part of the "Farrington-barracks group" that formed through a fission process 3 years before its transfer to the Wildpark Daun. In 1999 seven young animals (< 7 years old) from the Naturzoo Rheine were added to the colony (Jutta Küster, pers. comm.). At the time of the study the group comprised 42 animals including 8 adult males (7 prime males aged between 7 and 10 years and 1 one post-prime aged 15 years) and 16 adult females aged ≥ 5 years (see Appendix A). The group comprised one dyad of maternal brothers, but the relationship below this relatedness level was unknown.

Salem group

The second part of the study was conducted by A.B., N.B. and Elena Lange during the mating season 2006/07 (September to mid-February) at the Affenberg

Salem (Germany; for a history of the colony, see de Turckheim & Merz, 1984; Paul & Küster, 1988). The study group (H) was composed of 27 adult females (> 5 years old), 7 prime males (aged between 7 and 12 years old), 17 post-prime males (≥ 14 years old) and 6 juveniles. No subadult males were present at the time of the study (Table 4-1). The maternal relatedness among males was known from birth records, and maternal kin included three 3 dyads of brothers, 7 dyads of uncle/nephew and 7 dyads of cousins.

Animals in both groups lived in semi-free ranging conditions. In both parks, animals were fed daily with fruits, vegetables and grains that were distributed in different areas within the park. The monkeys also feed extensively on natural vegetation, including leaves, herbs, grasses and bark. Water was available *ad libitum*. From March to November tourists were allowed into both parks, but were restricted to path that runs through the area. All adult animals were recognized individually and habituated to the observers.

Behavioural observations

Daun group

Observational data were collected daily. A total of 258 hours of male focal data (Altmann, 1974) was collected by A.B., and 202 hours of female focal data was collected by C.B. The percentage of agreement (cf. Martin and Bateson, 2000) for focal sampling between A.B. and C.B. reached at least 85%. Male and female focal follows lasted 30 minutes and observation periods were randomized and equally divided among all the animals between morning and afternoon sessions. During male and female focal follows proximity scans were conducted every 5 minutes, whereby the locality (on the ground or in a tree) and activity (grooming, resting, locomotion, foraging) of the focal animal was noted, as well as the identity of all adult animals in body contact or grooming with the focal animal and of all adult animals within 2m, 10m and 30m. In addition to the standard protocol A.B. collected 88 hours of focal follows on attractive females (see below) from October until mid-February. These additional sessions were typically conducted at the end of the day. *Ad libitum* sampling (Altmann, 1974) was done by all observers throughout the day, whereby detailed information on sexual activities and agonistic interactions among adult animals were recorded.

Despite regular observations over a 6-month period, only 8 coalitions were recorded during the study period. The main observer (A.B.) observed 7 coalitions during 258 hours of male focal follow (0.03 or one per 37 hours). A focal male was involved in a coalitionary encounter as target or partner at a mean frequency of 0.007 event per hour (range: 0-0.03). Because the small number of coalitions observed precluded any statistical analyses, the data presented in the Methods section are for the Salem group, unless otherwise specified. We will come back to the Daun group in the discussion.

Salem group

Observational data were collected daily by A.B., N.B., and Elena Lange during the mating season 2006/07 (from the end of August until mid-February). A total of 279 hours of male focal data (Altmann, 1974), whereby detailed information on coalitionary interactions among adult males was recorded. The coalition data base was supplemented by *ad libitum* data (Altmann, 1974) which were recorded by A.B. and two additional observers (Elena Lange and Nicole Bischofberger) throughout the day. The inter-observer consistency could not be systematically tested due to the rapidity and unpredictability of coalition formation, but a good qualitative agreement was found among the three observers for the few coalitions that were observed simultaneously. The percentage of agreement (cf. Martin and Bateson, 2000) for focal sampling between A.B. and N.B., and A.B. and E.L. reached at least 80%. 56.8% of the coalitions that are used in this paper were collected by A.B.

Male focal follows lasted 15 minutes and observation periods were randomized and equally divided among all the adult males between morning and afternoon sessions. During male and female focal follows, proximity scans were conducted every 5 minutes, whereby the spatial locality of the focal animal (on the ground or in a tree) and its main activity (grooming, resting, locomotion, foraging) was noted, as well as the identity of all adult animals in body contact or grooming with the focal animal and of all adult animals within 2m, 10m and 30m.

In addition, a total of 373 hours of female focal data was collected by N.B, whereby detailed information on consortship behaviour by attractive females (see definitions below) was collected. In this study, a consortship is defined as an exclusive male-female dyad in which (i) close social proximity (<10 meters) and (ii) grooming, prolonged body contact and/or coordinated movements when walking were observed, and is restricted to mating periods (modified from Paul 1989). Only consortships lasting more than 5 min were included. Copulations between the consort partners were observed in more than 75% of all consortships and might have been only missed in the majority of the remaining cases due to incomplete sampling.

Definitions

A *coalition* was defined as simultaneous aggression directed by two partners against a common target (Box 1-1). “Scream-fights”, which are characterized by two primary antagonists screaming at each other and third parties joining the conflict as a response represent a separate phenomenon and were excluded from this study (see Chapter 1).

Coalition configuration (i.e. all-up, all-down, bridging: Fig. 1-1) was determined based on agonistic dominance ranks. Dyadic aggressive acts (open-mouth threat, lunge at, chase, slap, grab, bite) and approach/retreat interactions were used to construct the agonism matrix. If an agonistic interaction turned into a polyadic

interaction, only the sequence preceding the intervention of a third party was considered.

Table 4-1 Identity, rank, age and immigration status of the males of the Salem group

Male ID*	Ordinal Rank	Age	Natal status
Yak	1	14	Natal
Lud	2	12	Immigrant
Ron	3	11	Immigrant
Joh	4	7	Natal
Pun	5	16	Natal
Fli	6	9	Immigrant
War	7	10	Immigrant
Blo	8	15	Natal
Hul	9	20	Immigrant
Leo	10	10	Immigrant
Eyb	11	25	Natal
Fro	12	19	Immigrant
Pen	13	20	Immigrant
Fln	14	18	Immigrant
Neo	15	9	Immigrant
Ful	16	19	Immigrant
Sil	17	17	Immigrant
Wme	18	20	Immigrant
Pig	19	20	Immigrant
Luc	20	21	Immigrant
Fug	21	20	Immigrant
Ber	22	21	Immigrant
Tec	23	20	Immigrant
Cha	24	24	Immigrant

*The complete name and tattoo of the animals are provided in Appendix A.

Five *context of occurrence* were recognized for coalitions (modified from Noë 1989): 1. Over access to a receptive female: the immediate cause of the coalitionary conflict was competition between the target and one or both coalition partners over access to a receptive female. Barbary macaque females are receptive during distinct mating periods, which duration ranges from a few days to several weeks (Kuester & Paul 1992; this study).

2. Feeding context: the coalition occurred during a feeding session.

3. Third party coalition: the coalition formed, while the two partners interfered in an ongoing conflict between a male and a female or a juvenile, and attacked the male participant in that conflict.

4. Redirected coalition: the coalition formed after the two partners had been involved in a conflict against each other.

5. No apparent cause: the coalition did not fit any of the above categories and occurred without an immediate cause that was apparent.

A *consortship* was defined as an exclusive male-female dyad in which (i) close social proximity (<10 meters) and (ii) grooming, prolonged body contact and/or coordinated movements when walking were observed, and is restricted to mating periods (modified from Paul 1989). *Attractive females* were consorted at least 50% of their focal time (see details in Chapter 5).

In this study, we recognized two male age classes, namely *prime males* (aged 7-12 years) and *post-prime* males (aged > 12 years). Both classes of males were easily distinguishable by field observers based on their physical characteristics. Prime males were "athletic" and had their fully erupted canines intact, in contrast to post-prime males who were less muscular and generally showed worn or broken canines (Fig. 4-1).

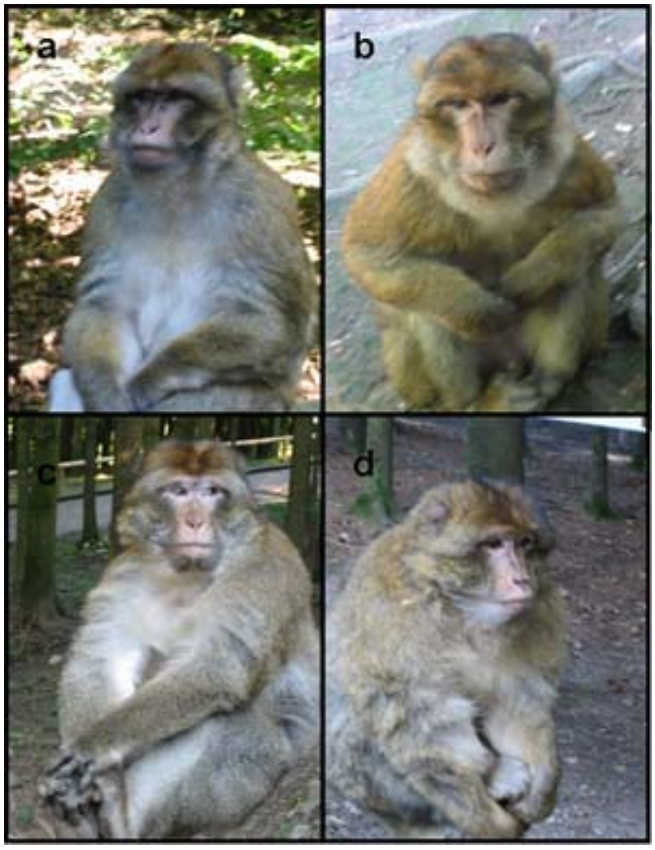


Figure 4-1 Prime males (a: 10 years old, b: 12 years old) and post-prime males (c: 17 years old, d: 22 years old) were easily distinguishable based on their physical appearance.

Results

General description of coalitions

A total of 111 coalitions were recorded in the Salem group during the study period. The main observer (A.B.) observed 37 coalitions during 279 hours of male focal follow (0.13 or one per 8 hours). A focal male was involved in a coalitionary encounter as target or partner at a mean frequency of 0.09 events per hour (0-0.32). The remaining coalitions were recorded *ad libitum* by three observers. All but 3 coalitions were formed by 2 partners and targeted at one male. Because we were mainly interested in the patterns of coalition formation rather than their frequencies, we pooled focal and ad libitum data from all three observers in the following analyses, unless otherwise specified.

86 coalitions were observed from the start. Parallel coalitions where two males simultaneously initiated aggression against a common target represented 62.8% (54/86) of the cases, whereas 37.2 % (32/86) were interference coalitions where one male intervened in an on-going escalated conflict (i.e. one that went beyond mere threats) and sided with one of the two opponents (cf. Box 1-1). Communication between the coalition partners before the attack was observed in 54.7% (47/86) of the cases. The silent-scream face, where the mouth is wide open and the lips are completely retracted (cf. Deag 1977; Fig. 4-2), was the most frequent signal used by the males (44/47). In nine additional cases, the partners looked at each other before launching the attack, which suggests that in most coalitions males were aware of the fact that their partner was instrumental in winning the interaction.

Figure 4-2 The silent-scream face in Barbary macaques, which is often used by males to recruit potential coalition partners.

Main characteristics of the coalition partners and their targets

A strong age pattern in coalition formation was found. Coalitions were mostly formed by older males and targeted at younger adults (Fig. 4-3). A prime male acted as a coalition partner in only 4 coalitions. Male age correlated positively with the rate of coalitions formed (Spearman correlation: r_s = 0.73, P <0.0001, N= 24) and negatively with the rate of being the target of one (r_s = -0.52, P =0.009, N= 24).

Male age was strongly correlated with rank, with younger adults occupying higher ranks than older adults (r_s=-0.70, P<0.001, N=24). However, age appears to be a better explanatory variable than rank, as the correlation between male rank and the rate of coalitions formed was weaker than that reported for male age (r_s=0.49, P=0.02, N=24) and no correlation between male rank and the frequency of being target of a coalition was found (r_s=-0.25, P=0.25, N=24; Fig. 4-4).

Coalition Configuration

All-up coalitions were the configuration most frequently observed (72%), whereas bridging (18.9%) and all-down (7.2%) occurred less frequently. One of the participants could not be identified in the remaining coalitions (1.8%).

Coalition contexts

The initial context of occurrence of coalitions was known for 85 of the 111 coalitions (Fig 4-5). An important part of the coalitions occurred without apparent cause or was observed during a feeding session, although food was clearly not limited. The 38 observed coalitions over access to a receptive female represented 34.2% of the coalitions. In most instances the contested female was sexually attractive to the males (see Methods). The target of the coalition was actually consorting the female in 73.7% (28/38) of the cases, and was competing with one or both coalition partners to get access to the contested female in the remaining cases (10/38). Almost half of the coalitions (16/38) were successful in terms of providing the coalition partners' access to the female. The dominant, younger coalition partner formed a new consortship and/or mated with the contested female after most (13/16) of the successful coalitions (average rank ± SEM of winner vs. loser: 11 ± 1.5 vs. 15.4 ± 1.6; average age ± SEM: 18.8 ± 0.9 vs. 19.4 ± 0.9), although the subordinate partner sometimes obtained priority-of-access (subordinate: 2 cases; both partners: 1 case).

We found evidence that coalitions may lead to the isolation of prime males during the mating season. Age was negatively correlated with time spent in the trees, i.e. prime males spent more time above ground than post-prime males (Pearson correlation: r = -0.81, P<0.0001; partial correlation coefficient controlling for rank: r = -0.73, P<0.0001, N=24). Moreover, the vast majority of consortships by prime males occurred in the trees (73/114) whereas the reverse was true for post-prime

males (8/122; Chi-square test: χ^2 (1) = 86.4, $P< 0.0001$). The spatial locality of consortships by prime males differed from what would be expected based on the time spent in each locality (Goodness-of-fit: $X^2(1) = 61.9$, $P< 0.0001$), whereas no significant pattern was found for post-prime males ($X^2(1) = 1.8$, $P= 0.18$; Fig 4-5). The observation that the vast majority of coalitions were initiated on the ground (92.8%, 103/111) and prime males were significantly more likely to be the target of coalitions when they were on the ground than in the trees (Goodness-of-fit: $X^2(1) = 4.2$, $P=0.04$; expected and observed values were calculated from male focal follows) suggests that coalitionary activity is likely to be responsible for the pattern observed.

One could argue that age per se (e.g. better physical condition or greater agility) may account for the reported pattern. According to this hypothesis, we would expect that in the Daun group where coalition formation was rare (see Methods) prime males also formed an important fraction of their consortships in the trees, all else being equal. In contrast to Salem, prime males in the Daun group were not significantly more likely to form their consortships in the trees than on the ground based on the time spent in each locality (Goodness-of-fit: $X^2(1) = 4.73$, $P=0.054$).

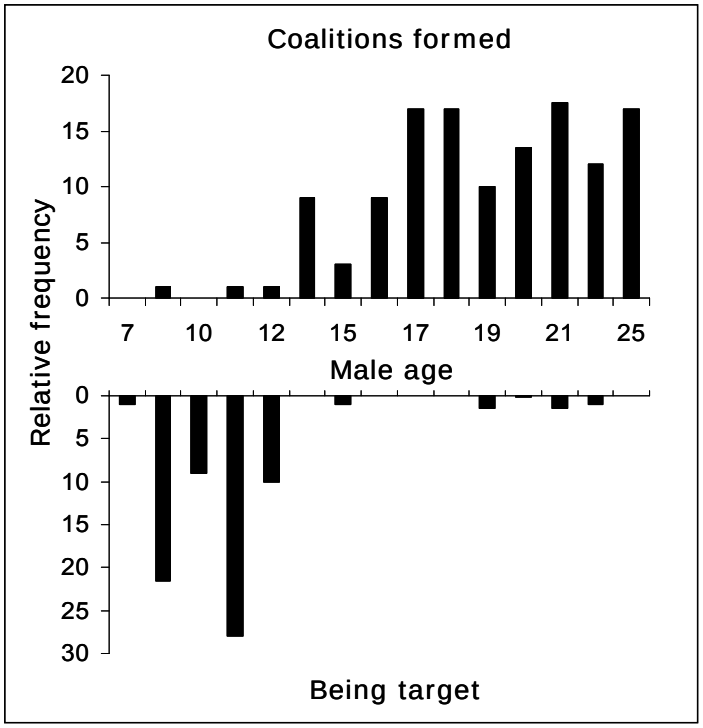


Figure 4-3 Frequency of participation in coalitions as partner (above) and target (below) according to male age.

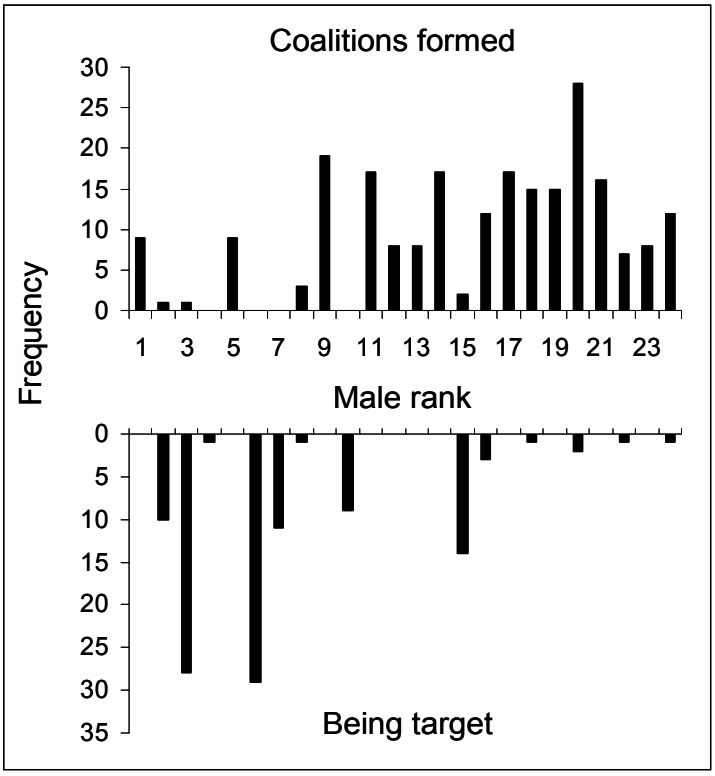


Figure 4-4 Same as above but according to male rank.

Moreover, the difference in the observed values was two times greater in the Salem than in the Daun group (Mann-Whitney: U=5, N_1=5, N_2=7, *P*= 0.04; Fig. 4-6). This discrepancy further supports the hypothesis that the prime males in Salem may have been driven into the trees by coalitions of post-prime males.

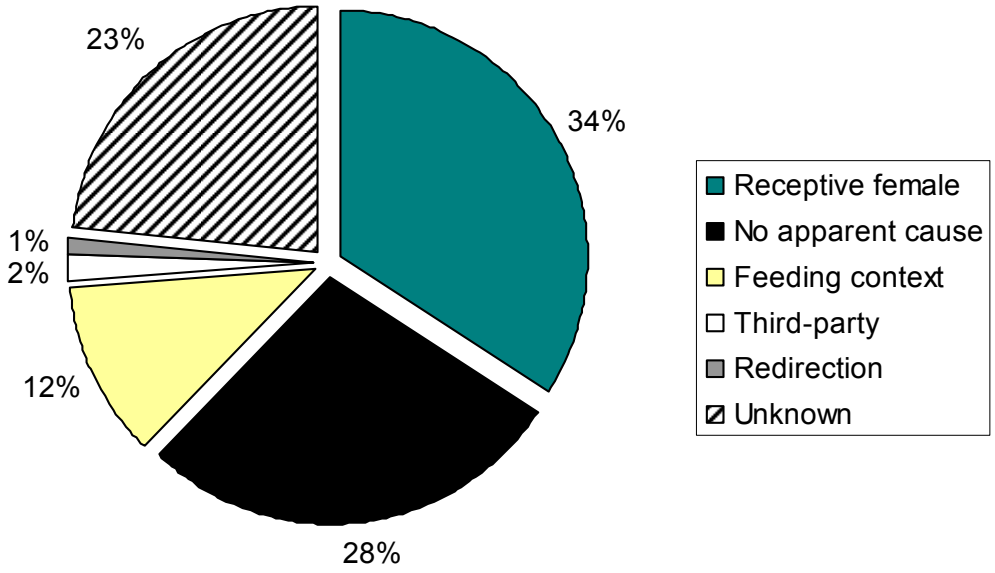


Figure 4-5 Initial context of occurrence of coalitions (*N*=111).

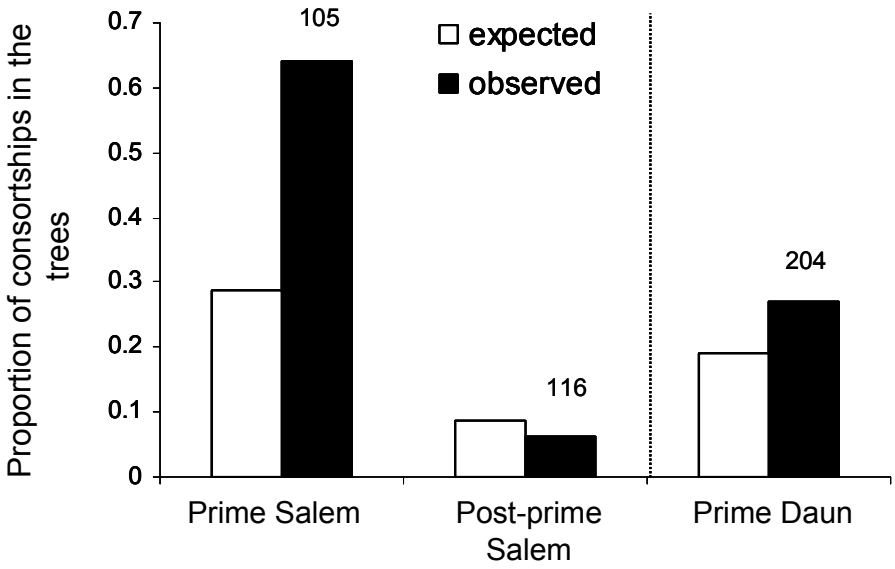


Figure 4-6 Proportion of consortships formed in the trees by prime and post-prime males of the Salem group, and prime males of the Daun group. The total number of consortships observed on the ground and in the trees is indicated.

Discussion

Primate males can use coalitions in different ways to improve their mating success (Smuts, 1985; van Schaik et al., 2006). Earlier studies in Barbary macaques suggested that males form coalitions during the mating season, but rarely do so to improve their rank (for a possible exception see Witt et al., 1981) or get instantaneous access to females (Kuester and Paul, 1992). In this study, we found evidence that males used all-up coalitions to level mating access in two different ways. First, coalitions over attractive females represented one-third of all coalitions. This type of coalitions has been extensively described in male savanna baboons (Bercovitch, 1988; Noë, 1992; Noë and Sluijter, 1995), but has been reported to be rare in previous studies of Barbary macaques (Taub, 1980; Kuester and Paul, 1992). This suggests that Barbary macaques show intra-species variation in that respect, although the reasons of this variation remain obscure (note: in Kuester and Paul's study males frequently formed coalitions, but rarely did so over access to females). The success rate of coalitions in producing a consort changeover was 42.1%, which lies within the range reported for male baboons (i.e. between 30-65%, Bercovitch, 1988; Noë, 1992, table 11.1). Unsuccessful changeovers sometimes occurred when the coalition was behaviourally unsuccessful (i.e. did not defeat the target, cf. Chapter 3). However, behaviourally successful coalitions did not always translate into mating access for the males, for example when females initiated a consortship with a third-party not

involved in the conflict, or re-established the previous consortship with the target of the coalition, as illustrated below (see also Kuester and Paul, 1992):

> At 14:22, Ron (aged 12 years, rank 3) sits on the ground. Mad (attractive female) approaches and presents to Ron, who inspects her. One minute later Ron performs an ejaculatory copulation with Mad and a grooming session ensues. The consorting pair stays in close proximity during the following 40 minutes. During this period Hul (aged 20 years, rank 9) sits within 30 m of the pair, but no other animal is in sight. At 15:02, Wme (aged 20 years, rank 18) is in sight. Hul directs a silent scream-face (i.e. recruitment signal) to Wme and both walk towards the consorting pair. Mad immediately moves away. Hul and Wme chase Ron who flees up in a tree. Wme leaves and Hul sits within 10 m of Mad. At 15:04, Mad climbs the tree and re-establish the consortship with Ron without Hul having copulated with Mad. Hul leaves the scene. (Female focal observation, 23 November).

This means that for males winning a coalitionary encounter only represented the first step towards mating success. In baboons, where female choice is limited (Alberts et al., 2003; Smuts, 1985), coalitions that failed to produce a consort changeover did so because of an aggressive response from the consort male (i.e. the coalition was behaviourally unsuccessful) or because the latter herded his female away from the males challenger (Bercovitch, 1988).

Second, an important part of the coalitions observed during the mating season occurred in the absence of any direct competition over females. Although we acknowledge that it will always be difficult to demonstrate the function of coalitions when no immediate effects are visible, we found clear evidence suggesting that males may use these coalitions as an offensive tactic to intimidate stronger competitors during the mating season, as suggested by Kuester and Paul (1992). Indeed, prime males spent more time in the trees than post-prime males and formed the vast majority of their consortships there, whereas the reverse was true for post-prime males. As we show in Chapter 5, the mating opportunities of prime males were mostly restricted to females visiting them in the trees. Because coalition partners initiated most coalitions on the ground and generally did not pursue the target when the latter retreated and sought refuge up in the trees (own obs.; see also Kuester and Paul 1992), it means that staying up above ground represented an efficient counter-strategy to coalitionary activity. Taub (1980) described a "peripheralization and attract strategy" in Barbary macaque males, which consists in a male attracting the attention of the female by displaying (e.g. branch shaking) and getting her to follow him, usually up in a tree, thus a voluntary behaviour. However, observations made in this and other studies (Witt et al., 1981; Paul, 1989; Kuester and Paul, 1992) indicate that peripheral males were aggressively expelled from the core of the group, "although they apparently often anticipate and avoid conflicts, and thus appear to steal away" (Paul, 1989, p. 471). Where, unlike in Salem, a group contains only a few post-prime males, the

peripheralization of subadults and lower-ranking, young adults would be achieved on a one-to-one basis (Witt et al. 1981; Paul 1989; own observations in the Daun group), whereas in the current study group at Salem, with its large cohort of post-prime males, higher-ranking, prime males were apparently driven away by coalitions of lower-rankers (see also Kuester and Paul 1992).

How can coalitions in the absence of any direct competition over females translate into mating benefits for the participating males? The most obvious answer is that by keeping stronger rivals away, lower-ranking males can increase their probability of getting access to females. Yet, in an fictitious group where the mating system functions as a queue (cf. Altmann, 1962, see Chapter 5) and coalitions by post-prime males are 100% effective in peripheralizing the top rankers (all prime), this tactic would mostly profit post-prime males ranking just below the targets, as shown in Fig 4-7. This occurs because coalitions produce a shift of the payoff curve towards the right (i.e. the top rankers being peripheralized, the male ranking right below them monopolizes all he can, and so on). Thus, we should expect middle ranking males to be mostly involved in this type of coalition, whereas males of lowest ranks should rarely if ever participate. However, Fig. 4-4 shows that males occupying low rank positions (e.g. rank 17 and below) frequently participated in coalition formation (a similar picture emerges if we remove the coalitions over direct access to females), and they apparently benefited from their behavior by obtaining matings (see Chapter 5). This suggests that leveling by lower-rankers can only occur in a system where queuing is not strictly enforced, i.e. if there is a scramble component to the acquisition of consortships and subsequently males participating in coalitions show restraint in challenging the consortships of each other. This is what is observed in Barbary macaques (Kuester and Paul 1992; this study, Chapter 5). Restraint in aggression among post-prime males was also apparent in the nature of the interventions performed during “scream-fights”, a common phenomenon during the mating season that we briefly describe in Chapter 1.

In savanna baboons a considerable number of coalitions also have no recognizable cause (Noë, 1990; 1992), although it remains unclear whether coalitions may serve a similar intimidating function in this species as suggested for Barbary macaques (Kuester and Paul 1992; this study). It has also been suggested that leveling may sometimes be at work in chimpanzees, when coalitions involving various combinations of lower-ranking males and targeting the top-ranking males are launched in the absence of any direct competition over females (van Schaik et al., 2006; cf. Goodall, 1986). It therefore remains to be determined whether other species may also use coalitions to intimidate higher-rankers into showing restraint in mating competition.

By only looking at coalitions over access to females, one could ask why the subordinate partner of the dyad even bothered to participate, giving that his chances of obtaining access to the female were very limited (about 10%, i.e. 50% chance of success in producing a changeover times 19% chance of access after a successful

changeover). In what may be an extreme case in baboons, for instance, some coalition partners obtained no direct consortship despite having participated in several winning coalitions over access to sexually receptive females (Noë 1990; but see Bercovitch 1988). By broadening the perspective, it becomes clear that mid-low rankers could benefit by using coalitions as a tool to intimidate higher-rankers into showing restraint in mating competition, although we acknowledge that no benefit of coalition formation is likely to contribute as much to individual fitness as gaining direct access to a female. Coalition formation apparently was a relatively low-risk tactic, as 0.9% (1/111) of coalitionary encounters resulted in mild injury (one partner had a bleeding nose; for similar observations in savanna baboons, see Bercovitch 1988). Thus, in a situation where there are some potential gains to all participants and costs are small, 'giving a try' is probably the best option available (Parker and Rubenstein 1981). A question that remains to be solved is whether why it pays for the post-prime males to show solidarity and together intimidate the prime males, rather than hold back and free-ride on the intimidation attempts by others (i.e. whether post-prime males face a social dilemma and if yes, how they solve it).

Another major finding of the study was that prime males hardly ever participated in coalitions. Coalitions in the Salem group were expressed in a strongly age-related fashion (Fig. 4-3), as reported in an earlier study (Kuester and Paul 1992). At similar ranks, younger males were much less likely than older males to participate in coalitions (compare for example post-prime males on rank 10 and 15 with prime males on rank 9 and 14, Fig. 4-4). Our observations in the Daun group confirm that prime males are rarely involved in coalitionary activity. At this stage we cannot provide any firm explanation to this age-related pattern in coalition formation, but can provide at least three non-exclusive hypotheses. First, coalitions are a complex behaviour that might need to be learned (Smuts, 1985; Noë and Sluijter, 1995; Alberts et al., 2003), which would explain why younger males do not express this behaviour until middle age (cf. Smuts, 1985; Alberts et al., 2003; but see Noë and Sluijter, 1995). Second, rank is generally age dependent in primate males (Paul, 1989; Sprague, 1998; Packer et al., 2000; Brauch et al., 2008) and challenges for the top position are more likely to occur when males are in their prime and thus at the peak of their physical condition (reviewed in van Noordwijk and van Schaik, 2004a). Thus, it may be advantageous for prime males to avoid open conflicts and the risk of being heavily injured as this might jeopardize their chances of ever achieving top dominance, which is the period during which the greatest contribution to lifetime reproductive success is accrued (van Noordwijk and van Schaik, 2001). Third, there is growing evidence that tolerance constrains the ability of individuals to cooperate (Petit et al., 1992; Melis et al., 2006; Hare et al., 2007), and it is possible that age differences in the strength of the social relationships conform to age differences in coalitionary behaviour (e.g. Smuts and Watanabe, 1990; Smuts, 2002). The observation that prime males in the Salem group were less likely to be in proximity to other males than post-prime males (Mann-Whitney: U= 27, P=0.039) and were almost never seen at the feeding sites in company of others (own observations) would

provide support for this hypothesis. This issue will be addressed with the appropriate proximity and affiliative data in a future work (A.B. in prep.). Regardless, an important consequence of this age-dependence of participation in coalitions is that the demographic structure of a group now becomes an issue to be examined both empirically and theoretically as it is bound to affect the incidence and effectiveness of all-up leveling coalitions (see Chapter 6).

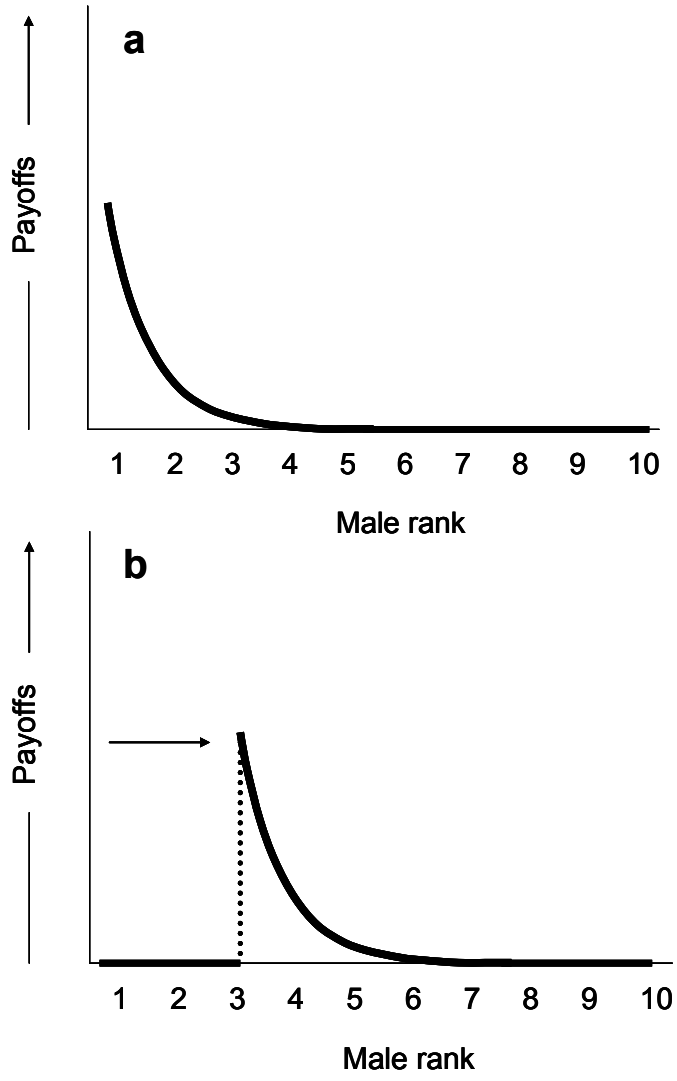


Figure 4-7 In an fictitious group where the mating system functions as a queue, the top-rankers (prime males) gain the lion's share of the matings (a). If in the same group all-up coalitions by post-prime males were 100% effective in peripheralizing the top rankers, this tactic would mostly profit males ranking just below the targets (b).

Chapter 5

Mating skew in males Barbary macaque: the role of cycle synchrony, female behavior and male coalitions

A fundamental question of sexual selection theory concerns the causes and consequences of reproductive skew among males. The priority of access (PoA) model (Altmann 1962) has been the most influential framework in primates living in permanent, mixed-sex groups, but to date it has only been tested with the appropriate data on female synchrony in a handful of species. In this paper, we used mating data on one semi-free ranging-group of Barbary macaques: (1) to provide the first test of the priority-of-access model in this species, and (2) to determine the proximate mechanism(s) underlying male mating skew. Our results show that the fit of the observed distribution of matings with attractive females to predictions of the PoA model was poor, with males ranked 5-24 mating more than expected. While our work confirms that female cycle synchrony sets an upper limit to monopolization by dominant individuals, other factors are also important. Coalitionary activity was the main alternative tactic used by males to lower mating skew in the study group. Coalitions were expressed in a strongly age-related fashion and allowed subordinate, post-prime males to increase their mating success by targeting more dominant, prime males. Conversely, females, while mating promiscuously with several males during a given cycle, were more likely to initiate their consortships with prime males, thus reducing the overall effectiveness of coalitions. We conclude that dominant Barbary macaque males have a limited ability to monopolize reproduction, leading to modest reproductive skew among them.

Introduction

The causes and consequences of reproductive skew, the extent to which breeding is monopolized by dominant individuals, have received much theoretical and empirical attention in the last few decades (reviewed in Johnstone, 2000). Reproductive skew theory has been divided in two broad categories (reviewed in Clutton-Brock, 1998; Johnstone, 2000; Kutsukake and Nunn, 2008). Transactional models propose that reproduction is controlled by the dominant individual, who allows the subordinates to reproduce to a certain extent as a staying incentive (Clutton-Brock, 1998; Johnstone, 2000; Keller and Reeve, 1994), whereas limited control or compromise models suggest that the dominant individual is unable to completely prevent the reproduction by subordinates completely (Cant, 1998; Clutton-Brock, 1998; Reeve et al., 1998). Empirical studies have provided mixed results for variants of both models in species of social insects, cooperatively breeding birds, and mammals (reviewed in Magrath and Heinsohn, 2000; Reeve and Keller, 2001; Clutton-Brock et al., 2001).

In primates, the priority-of-access model (i.e. PoA, Altmann, 1962), which can be viewed as a special case of the more general limited-control models of reproductive skew (Kutsukake and Nunn, 2008), has been commonly used to set the basic expectation of mating skew among males. This model states that the degree to which the dominant male monopolizes reproduction within a group is affected by the number of simultaneously cycling females. When two females are in estrous simultaneously, the alpha male is unable to monopolize both of them effectively, thus allowing the beta male to mate, and so on. Variability in male mating and reproductive success should thus be a function of male dominance rank and the number of simultaneously estrous females. To date, the predictions of the PoA model have only been tested with the appropriate data on female synchrony for a handful of species (baboons: Hausfater, 1975; Altmann et al., 1996; Alberts et al., 2003; Weingrill et al., 2003; chimpanzees: Boesch et al., 2006; Wroblewski et al., 2009; Japanese macaques: Hayakawa, 2007; rhesus macaques: Chapais, 1983c; mandrills: Setchell et al., 2005). These studies have shown that the ability of dominant males to monopolize females decrease with increasing female synchrony, in line with the PoA model. On the other hand, a lack of perfect fit with the predictions of the PoA model suggest that in addition to female synchrony other factors can limit monopoly by dominant individuals. For example, male alternative mating tactics such as the formation of "leveling" coalitions (sensu van Schaik et al., 2004a) can effectively lower mating skew by allowing subordinate males to usurp females from more dominant rivals as shown for male savanna baboons (Bercovitch, 1988; Noë and Sluijter, 1990; Noë, 1992; Alberts et al., 2003). Moreover, some females may prefer middle- or lower-ranking males (e.g. rhesus macaques: Chapais, 1983a; ringtailed

lemurs: Pereira and Weiss, 1991; Japanese macaques: Soltis et al., 2001; Hayakawa, 2007; chimpanzees: Stumpf and Boesch, 2005; Stumpf and Boesch, 2006) or prefer to mate with several males (e.g. long-tailed macaques: Nikitopoulos et al. 2005; Engelhardt et al. 2006), thus decreasing skew.

Barbary macaques represent an interesting system in which to investigate the applicability of the PoA model. They live in multi-male multi-female groups of up to 88 individuals in natural populations (Fooden, 2007) and show a distinct mating season restricted to autumn and winter in natural and food-enhanced populations (reviewed in Fooden, 2007). Typically, several females in the same group are sexually active concurrently (Paul, 1989; Small, 1990; Kuester and Paul, 1984, 1992; Brauch et al., 2008) and high conception rates have been reported to occur in a one-month period (e.g. Kuester and Paul, 1984; Small, 1990). Kuester and Paul (1992) concluded that the high number of simultaneously cycling females puts Barbary macaque males in an extreme "time budget dilemma" (cf. Bercovitch, 1987) by reducing the benefits associated with continuous monopolization of a single female. However, the extent to which female cycle synchrony represents the main factor reducing skew in Barbary macaques remains to be determined.

Moreover, Barbary macaque males form coalitions in the context of mating competition (Witt et al. 1981; Kuester and Paul 1992; Chapter 4), although intra-species variation linked to group demography has been documented (Chapter 4). Coalitions are the almost exclusive domain of post-prime males and are mostly targeted at prime males (Kuester and Paul 1992; Kuester and Preuschoft unpublished manuscript; Chapter 4), but other age classes may sometimes be involved (Witt et al., 1981; Paul, 1989). Since younger adults are generally higher ranking than older adults (Kuester and Paul 1992; Kuester and Preuschoft unpublished manuscript; this study), most coalitions are directed up the hierarchy (cf. "all-up" coalitions, van Schaik et al., 2004). In Chapter 4, we suggested that coalitions are used by males to usurp attractive females from prime males and as an offensive tactic to intimidate these males resulting in them being isolated up in the trees (see also Kuester and Paul, 1992). However, whether coalition formation represents a major alternative tactic allowing lower-ranking males to decrease skew, as suggested in savanna baboons (Alberts et al., 2003), remains to be determined.

Furthermore, female Barbary macaques play an active role in initiating and terminating their consortships, mate with multiple males during both their non-fertile and fertile periods, and are generally cooperative with all potential mates (Kuester and Paul, 1992; Menard et al., 2001; Paul et al., 1993; Taub, 1980; Small, 1990; Brauch et al., 2008). Many authors concluded that a lack of female choice or partner preference is characteristic of this species (Kuester and Paul, 1992; Small, 1990; Taub, 1980), although Brauch et al. (2008) provided evidence of female mate choice for higher-rankers. Thus, it appears that Barbary macaque females can be promiscuous, thus decreasing male mating skew, or "choosy", thus increasing mating skew. The reason for this variation across studies remains unclear.

The aim of this paper is to understand to which extent female cycle synchrony, female mating behavior and male-male coalitions influence male mating skew in one semi-free ranging group of Barbary macaques. We addressed the following three questions: (1) To which extent can the PoA model account for the distribution of matings among male ranks in the study group? (2) Does coalition formation represent a major alternative reproductive tactic allowing lower-ranking males to decrease skew? (3) Does female mating behavior contributes to increasing or decreasing mating skew among males? In many species, the conflicting strategies of the two sexes interact to produce mating and reproductive outcomes (e.g. Manson 1992; Soltis et al. 1997). This study provides a clear example of how the observed skew among males can be a compromise between male and female mating efforts.

Methods

Study site and study group

The study group inhabited a forested enclosure of 14.5-ha at the Affenberg Salem, Germany (for a history of the colony, see de Turckheim and Merz, 1984). Animals were fed once daily with fruits, vegetables and grains distributed in different areas within the park. The monkeys also fed extensively on natural vegetation, including leaves, herbs, grasses and bark. Water was available *ad libitum*. From March to November tourists were allowed into the enclosure, but were restricted to a path.

The study group (H) was composed of 27 adult females (> 5 years old), 7 prime males (aged between 7 and 12 years old), 17 post-prime males (≥ 14 years old) and 6 juveniles. No subadult males were present at the time of the study. All adult animals were recognized individually and habituated to the observers.

We recognized two male age classes, namely *prime males* (aged 7-12 years) and *post-prime* males (aged > 12 years). Both classes of males were easily distinguishable by field observers based on their physical characteristics. Prime males were “athletic” and had intact, fully erupted canines, in contrast to post-prime males who had a less muscular build and generally showed worn or broken canines (see Fig. 4-1).

Sampling method

Observational data were collected daily by A.B. and Nicole Bischofberger during the mating season 2006/07 (from the end of August until mid-February). A total of 279 hours of male focal data (Altmann, 1974) was collected by A.B., and 373

hours of female focal data was collected by N.B. The percentage of agreement (cf. Martin and Bateson, 2000) for focal sampling between A.B. and N.B. was tested in four focal sessions of 15 minutes and reached at least 80%. In addition, *ad libitum* sampling (Altmann, 1974) was done by both observers throughout the day, whereby detailed information on sexual activities and agonistic interactions among adult animals were recorded. Most analyses presented in this paper are based on female follows.

Focal females were selected based on three criteria relating to female attractiveness: (1) the occurrence of sexual behaviour (sexual calls, inspections, presentations, copulations); (2) the presence of males in vicinity of the female; and (3) a qualitative assessment of the swelling change. These criteria were evaluated daily, several times per day, by two to three observers. Females were then followed as long as males showed interest in them and on one additional day following the "attractiveness breakdown" (cf. Chapais, 1983; Kuester and Paul, 1984). Observation time was equally divided when more than one female was attractive and balanced between morning and afternoon sessions. Depending on the number of attractive females, female focal follows could last from one to four hours (median: one hour).

Hormonal implants

For management purposes the majority of the adult females (n=20) had been implanted with a hormonal contraceptive (Norplant®, active ingredient: Levonorgestrel) one month to 10 years before the start of the current study (Table 5-1). In humans levonogestrel implants prevent pregnancy nearly perfectly for 3 to 5 years (Sivin et al., 1997; 2001; Glasier, 2002). The contraceptive effect is achieved through a variety of mechanisms that range from anovulation to insufficient luteal phase (Croxatto, 2002). The impact of levonogestrel implants on female attractivity in Barbary macaques during the mating season has not yet received systematic empirical attention (Wallner et al., 2007) for the effects of levonogestrel implants on swelling size in Barbary macaques outside the mating season), but Small (1990) mentioned that most of the implanted females in a group of semi-free ranging Barbary macaques (Rocamadour, France), "showed no signs of estrus" (p.271) during the mating season.

In the study group, a mixed pattern was observed. 13 implanted females and 2 non-implanted females showed very low levels of sexual activity during the mating season (e.g. range of ejaculatory copulations: 0-10, median: 0, all sampling sources combined), and the lack of a strict temporal pattern of sexual activity was found in one additional female (i.e. 18 isolated ejaculatory copulations were spread over a period of one month and a half). These 16 females were thus excluded from the analyses. Six implanted females were attractive to males and showed clear periods of mating and consorting activity, separated by periods without any sexual activity, as observed in naturally cycling females. 11 mating phases (1-2 per female) were identified in the 6 implanted females (mean length/female: 10.7 days, range: 5-24)

and 8 mating phases (1-3 per female) in the 5 non-implanted females (mean length/female: 18.9 days, range: 8-28). Overall the matings phases were shorter in implanted than non-implanted females, but the difference failed to reach statistical significance (Mann-Whitney, n=11, U=5.5, p=0.082). Most importantly for the purposes of this study, no significant difference was found between the implanted and non-implanted females in female attractivity in the mating phase (mean hourly rate of ejaculatory copulation ± SEM, non-implanted females: 1.30 ± 0.23, implanted females: 1.26 ± 0.27, Mann-Whitney, n=11, U=14, p=0.86; Fig. 5-1; mean proportion of time spent in consortship, non-implanted females: 0.45 ± 0.05, implanted females: 0.55 ± 0.09, n=11,U=11, p=0.47). Thus, we assumed that the males did not differently perceive the 6 implanted and 5 non-implanted females and we included all the 11 females in the analyses.

Table 5-1 Age, rank, parity and implant status for the study females.

Female ID[1]	Age	Rank[2]	Parity	Implanted since	Focal time (h)
Hub	5	High	Primiparous	1 year	-
Tri*	6	Mid	Primiparous	2 years	36.75
Mum*	6	High	Multiparous	1 month	23.25
M2d*	7	High	Primiparous	2 years	90.5
Sla	8	High	Primiparous	2 years	15.25
Ali	10	High	Primiparous	2 years	-
Lol*	12	Mid	Primiparous	Not implanted	52.25
Bla*	15	Low	Nulliparous	Not implanted	16.75
Col	15	High	Multiparous	4 years	-
Fan	15	Low	Nulliparous	11 years	-
Blu*	17	Low	Nulliparous	Not implanted	14.75
Mad*	17	Mid	Nulliparous	Not implanted	33
Fet*	18	Low	Nulliparous	10 years	8.5
Jan	18	High	Multiparous	5 years	-
Man	19	Mid	Nulliparous	5 years	6
Wst*	19	Mid	Nulliparous	Not implanted	41.75
Bon	20	Low	Nulliparous	Not implanted	-
Her	20	Low	Primiparous	2 years	1.5
Ste*	20	Low	Primiparous	2 years	12.5
Dir*	21	High	Primiparous	2years	-
App	22	Mid	Primiparous	2 years	-
Bea	22	High	Primiparous	5 years	-
But	22	Mid	Primiparous	2 years	-
Duk	23	Low	Primiparous	2 years	-
Eyl	23	Low	Primiparous	Sterile	-
Ala	23	Mid	Nulliparous	5 years	-
Omi	29	Low	Multiparous	Not implanted	-

*Females included in the analyses

[1] The complete name and tattoo of all animals is provided in Appendix A.

[2] The dominance rank of females was determined from all occurrences of dyadic interactions.

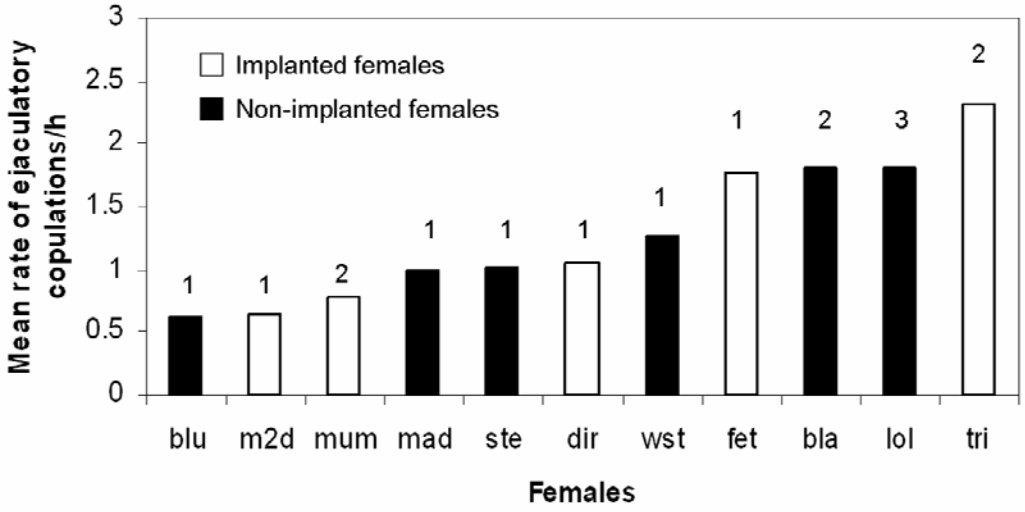


Figure 5-1 Mean rate of ejaculatory copulations per hour of focal observation for the implanted and non-implantedfemales included in the study. The number of mating phase(s) from which the mean hourly rates were calculated are indicated.

Dominance ranks

Dyadic aggressive acts (open-mouth threat, lunge at, chase, slap, grab, bite) and approach/retreat interactions were used to construct a dominance matrix. If an agonistic interaction turned into a polyadic interaction, only the sequence preceding the intervention of a third party was considered. The program Matman (de Vries et al. 1993) implemented in Excel was used to generate the ordinal rank order among the males. Despite the large number of males, a significantly linear hierarchy was found in the study group (Landau's linearity index corrected for unknown relationships: 0.46, $P < 0.0001$). The percentage of bidirectional relationships was 12.3%, whereas 36.2% of male-male relationships remained unknown. The alpha position was occupied by the same male (Yak, aged 14 y.o.) since at least two years before the beginning of the current study (staff of the Affenberg, pers. comm.). Dominance ranks of males were strongly correlated with age, with younger adults occupying higher ranks than older adults (r_s=-0.70, P<0.001, N=24; Table 2). For females only classes of dominance (high, mid, low) could be determined due to small sample size.

Definitions

Consortship: an exclusive male-female dyad in which (i) close social proximity (within 10m) and (ii) grooming, prolonged body contact and/or coordinated movements when walking were observed, and is restricted to mating periods (modified from Paul 1989). Only consortships lasting more than 5 min were included. Copulations between the consort partners were observed in more than 75% of all

consortships and might have been only missed in the majority of the remaining cases due to incomplete sampling.

A *changeover in consortship* typically occurred through the direct switch of a female from the ex-consorting partner to a new partner (i.e. *challenger male*). However, changeovers were not always direct, i.e. a consortship between male A and a female could be followed by the female being in a non-consortship with male B (minimal criterion: male B was the only male within 10m of the contested female), before a new consortship was formed with male C. In such cases of "indirect changeovers" we examined the pattern of behavior between male B and C, because we considered that male B was the main rival of C at the time C established its consortship.

Either the male challenger or the female may be responsible for the *initiation of the new consortship*. The initiator of a consortship was defined as the animal that made the approach (i.e. walked to within 2m of another individual) resulting in the establishment of a consortship (cf. Taub 1980, p. 293). When the consort took place in the trees, typically the female climbed the tree where a male was resting alone; we attributed the initiation of the consortship to the female, even in the rare cases where it was the male who made the final approach to within 2m. When both animals approached each other simultaneously, the consortship was considered to have been mutually formed.

To investigate the behavioral factors responsible for the mating success of individual males, we determined the activity pursued by the male challenger in the context of changeovers in consortships. Seven behavioral categories for changeovers in consortships were defined (modified from Noë and Sluijter, 1990).

1. Solo changeover: the male challenger obtained access to the female after a dyadic agonistic conflict with a rival male. The rival male was usually the previous sexual partner (i.e. direct changeover), but cases where males competed over an unattended female were also observed. An agonistic conflict is defined as any interaction between two individuals in which at least one agonistic behavioral element (threat, attack) was shown.

2. Coalitionary changeover: the male challenger obtained access to the female by forming a coalition or using the threat of coalition against the previous sexual partner. *Coalition* was defined as joint aggression between at least two males against a common target (in consort with a single male for >95% of observation time, cf. Engelhardt et al., 2006), often preceded by signaling between the attackers. Barbary macaques signal their intention to form a coalition mainly by performing a silent-scream face, where the mouth is wide open and the lips are completely retracted so showing the teeth (cf. Deag, 1974, see Fig. 4-2). Prolonged glances can concurrently be made at other individuals (e.g. "show-looking": de Waal et al., 1976; "head-flagging": Packer, 1977). "Scream-fights", which are characterized by two primary antagonists screaming at each other and third parties joining the conflict as a response (see Chapter 1), represent a separate phenomenon and were excluded from this study.

The *threat of coalition* is defined as the use of signaling (see above) between the male challenger and one or more males, which did not translate in the formation of a coalition but was immediately followed by the previous male partner walking away from the female.

3. Opportunistic changeover: the male challenger obtained access to a female after one or more adult males directed aggression against the previous male partner (i.e. solo aggression or coalition), but without the male challenger to be involved in the conflict himself.

4. Coercive changeover: the male challenger obtained access to a female by displacing, lunging at or chasing the female, thus herding her away from rival male(s).

In many instances the male challenger obtained access to a female in the absence of any apparent agonistic conflict among the rival males. We divided these "aggression-free" changeovers in two categories. 5. *Avoidance* leading to changeover was scored when an ongoing association between a male and a female was terminated either because the female partner walked away from its partner and moved near or approached a male rival, or the ex-mating partner stopped following or walked away from its female partner in response to a male challenger moving toward the pair. It was important that the previous male partner was still showing interest in the female at the time of the changeover (i.e. he was grooming or following her). 6. *Abandonment* was scored if the ex-mating partner voluntarily moved away from the female or did not follow its female partner, but this was not due to the female partner approaching a male rival or in response to a male challenger moving toward the pair.

7. *Other*: Changeovers that did not easily fit to the categories described above were put together in this category.

Consortship: an exclusive male-female dyad in which (i) close social proximity (<10 meters) and (ii) grooming, prolonged body contact and/or coordinated movements when walking were observed, and is restricted to mating periods (modified from Paul 1989). Only consortships lasting more than 5 min were included. Copulations between the consort partners were observed in more than 75% of all consortships and might have been only missed in the majority of the remaining cases due to incomplete sampling. A *changeover in consortship* typically occurred through the direct switch of a female from the ex-consorting partner to a new partner (i.e. *challenger male*). However, changeovers were not always direct, i.e. a consortship between male A and a female could be followed by the female being in a non-consortship with male B (minimal criterion: male B was the only male within 10m of the contested female), before a new consortship was formed with male C. In such cases of "indirect changeovers" we examined the pattern of behavior between male B and C, because we considered that male B was the main rival of C at the time C established its consortship.

Either the male challenger or the female may be responsible for the *initiation of the new consortship*. The initiator of a consortship was defined as the animal that

made the approach (i.e. walked to within 2 meters of another individual) resulting in the establishment of a consortship (cf. Taub 1980, p. 293). A consortship was established when the partners started grooming (the grooming bout was usually followed by a copulation) or when the first copulation was observed. When the consort took place in the trees, typically the female climbed the tree where a male was resting alone; we attributed the initiation of the consortship to the female, even in the rare cases where it was the male who made the final approach to within 2 meters. When both animals approached each other simultaneously, the consortship was considered to have been mutually formed.

Testing the priority-of-access model

Female attractive and peri-ovulatory days

In this paper, we attempt to measure the mating success of males with females that are attractive for them. Due to the infertility of most females, no effort is made to estimate the actual siring success of males. The *attractive days* were identified based on the time spent in consortship, as we assumed that this parameter probably represents the best indicator of males' willingness to invest time and energy in a female. This is further justified by the observation that consortships in Barbary macaque are maintained mostly by males (Heistermann et al. 2008). Thus, males almost always followed the female while in locomotion while the reverse was extremely rare (Kuester & Paul, 1992; own observation).

A female's attractivity is a continuous variable that we had to dichotomize into "attractive" and "non-attractive" for each day to make it tractable. The total time spent in consortships during female focal follows ranged from 0 (not consorted) to 1 (consorted during the entire focal session). The cut-off point was arbitrarily set at 0.50, i.e. we considered that a female which was consorted at least 50% of its focal time was attractive for the males and included as "attractive days" all female-days with values equal to- or higher than 0.50. The hourly rate of ejaculatory copulation of females was higher on attractive than non-attractive days, which justifies the above decision (hourly rate of ejaculatory copulations/female ± SEM, non implanted females, "attractive days": 1.62 ± 0.28 *versus* "non attractive days": 0.64 ± 0.11, Wilcoxon signed rank test, n= 5, z= -2.023, p=0.043; implanted females: 1.47 ± 0.28 *versus* 0.89 ± 0.20, Wilcoxon signed rank test, n= 5, z= -2.02, p=0.043).

A second, independent way to operationalize attractivity is to restrict it to peri-ovulatory days. The *peri-ovulatory period* was identified for each female cycle based on the day of attractivity breakdown (Kuester and Paul, 1992), as it represents a reliable indicator of the time of ovulation in this species in the absence of endocrinological data (M. Heistermann, pers. comm). The diagnostic behavioral criterion of the attractivity breakdown is a steep decrease (or complete cessation) of copulations, consortship activity and male inspections of females (Kuester and Paul 1984; Heistermann et al. 2008). The peri-ovulatory period was identified in implanted

and non-implanted females as follows: we identified a 3-day window in which ovulation was more likely (day -2 to day -4 from attractivity breakdown) and defined the peri-ovulatory period as the period comprising these 3 days plus the 3 preceding days in order to account for sperm survival in the female's reproductive tract (i.e. day -2 to day -7). We applied this procedure to both implanted and non-implanted females, despite the (likely) absence of ovulation in the former. The day of attractivity breakdown could be precisely determined in 13 out of 19 peri-ovulatory periods and was assigned in the 6 remaining periods with a possible margin of error of ± 1 day.

Calculating expected mating success

We assigned expected mating success based on the priority-of-access model following Altmann (1962). The expected proportion of ejaculatory copulations for each male rank over the study period was calculated as follows: the expected proportion of ejaculatory copulations by the alpha male equaled the number of days that at least one female was attractive/peri-ovulatory, divided by the total number of female attractive/peri-ovulatory days; the expected proportion by the second male equaled the number of days that at least two females were attractive, divided by the total number of female attractive/peri-ovulatory days; and so on for lower-ranking males. This operationalization reflects the PoA model, in that is assumes that a male is able to monopolize only one female on a given day, and that he alone should be responsible for all ejaculatory copulations observed with that female on that day. The *observed* proportion of ejaculatory copulations for individual males equaled the number of ejaculatory copulations that a male performed with a female on a given attractive/peri-ovulatory day, divided by the total number of ejaculatory copulations performed by all males with that female on that day. These daily proportions were summed up for each male over all female attractive/peri-ovulatory days, and divided by the total number of female attractive/peri-ovulatory days to give an observed mating success per male rank over the study period.

Kuester and Paul (1994) provided evidence for a strong mating inhibition between co-residing maternal relatives, including brother/sister dyads and uncle/ niece dyads. As a consequence, the expected values for the alpha and beta males were calculated by excluding their maternal relatives as potential mates (e.g. when only one of the alpha male's maternal relative was attractive/peri-ovulatory, the beta male was expected to monopolize her).

Statistics

Logistic regression (Quinn and Keough, 2002) was used to determine if females were more likely to initiate their consortships according to male age or rank. The responsibility in consortship initiation was determined as explained above (coded 1 if initiated by female and 0 if initiated by a male). Age was known from birth records and is a continuous variable. Rank was determined as explained above and is an ordinal variable. Because individuals contributed more than one data point in the

data set, we included a random effect for the male partner and the female partner. Logistic regressions were performed with the help of the program R v. 2.6.0 (R Development Core Team 2008).

The lambda and beta indices (see below) were calculated with the Skew Calculator 2003 available online at: www.obee.ucla.edu /Faculty/Nonacs. The remaining analyses were performed with the statistical package SPSS 14.0. Continuous variables used in the Pearson correlation tests were tested for normality with the Shapiro-Wilk test before performing the analyses. All remaining tests were non-parametric. The significance level alpha was set to 0.05.

Results

Female synchrony

The mating season started on October 20th, when two females showed the beginning of their first mating period, and ended on February 8th with the end of the last mating period. During the mating season, attractive or peri-ovulatory females were present on 73.6.2% and 56.3% of the focal observation days, respectively. Up to 4 or 5 females were simultaneously attractive or peri-ovulatory, but on 45.3% of attractive days and 65.3% of peri-ovulatory days no other female was attractive/peri-ovulatory. Thus, there were always more adult males present then there were attractive/peri-ovulatory females, i.e. the operational sex ratio was always strongly biased in favor of males. The observed mating success of males on peri-ovulatory days and attractive days was very highly correlated (Spearman correlation, r_s=0.955, P<0.001, N=24).

Priority-of-access model

Complete monopolization (in consort with a single male for >95% of observation time, cf. Engelhardt et al., 2006) of an attractive/peri-ovulatory female was only achieved by the dominant male with the beta female (implanted). This pair was seen together from Oct. 20th until Nov. 27th, with a 3-day interruption (26th- 28th October) where the female was seen to copulate with 4 other males. During the monopolization period, the dominant male completely ignored the cycle of 2 unrelated, non implanted females. In the remainder of the mating season the dominant male achieved matings with other females during shorter, non-exclusive consort bouts.

Figure 5-2 shows the predicted proportion of ejaculatory copulations for each male of each rank, calculated using the priority-of-access model, for all attractive days (Fig. 5-2a) and peri-ovulatory days (Fig. 5-2b). Both graphs show that the quantitative fit of the data to the priority-of-access model is poor, with males ranked 5-24 mating

more than expected. To determine the extent of mating skew in the study group, we used the "lambda" index of mating skew (Kokko and Linstrom, 1997). Lambda ranges from 0 (mating evenly distributed) to 1 (mating completely skewed towards one male). The lambda index indicates that mating skew is rather low in the study group (lambda index, attractive days: 0.15; peri-ovulatory days: 0.16; illustrated by the shallow shape of the observed distribution of matings in Fig. 5-2). When we tested the distribution of mating against a null hypothesis of random mating within the group using the B index (random mating within the group is indicated by B=0 and a positive value indicates that skew is greater than expected, cf. Nonacs 2000; 2003), we find that the distribution of mating was significantly skewed among the males (attractive days: 0.04, P=0; peri-ovulatory days: 0.04, P=0).

The presence of a correlation between male rank and mating success on both attractive and peri-ovulatory days (attractive days, Spearman correlation: r_s=-0.74, P<0.001, N=24; peri-ovulatory days: r_s= -0.70, P<0.001, N=24; rank of alpha male = 1) confirm that higher-rankers had an advantage in mating competition, albeit much less than expected based on the PoA model. Since male age and rank were closely related in the study group with younger adults occupying higher ranks (cf. Table 4-1), male age and male rank were equally good at predicting male mating success (with age: attractive days, r_s=-0.78, P<0.001, N=24; peri-ovulatory days: r_s= -0.75, P<0.001, N=24).

Behavioral mechanisms decreasing skew: the male perspective

In an attempt to determine the proximate mechanism(s) that led to the lower than expected mating skew, we examined the tactics used by male challengers in the context of changeover in consortships. We distinguished between the consortships acquired by dominant male challengers from subordinate rivals and those acquired by subordinate challengers from dominant rivals. The latter are of particular interest because they contributed to decreasing mating skew (i.e. the matings went "down the hierarchy"). Only confirmed successful consortship changeovers (i.e. which led to at least one ejaculatory copulation by the male challenger) were used for the analyses. The analyses were performed for access to attractive and peri-ovulatory females, but because very similar results were obtained for both data sets (unpublished results), we only present the analyses of 193 successful changeovers over females on their attractive days. Figure 5-3 shows the frequency of male tactics that produced a changeover in consortships.

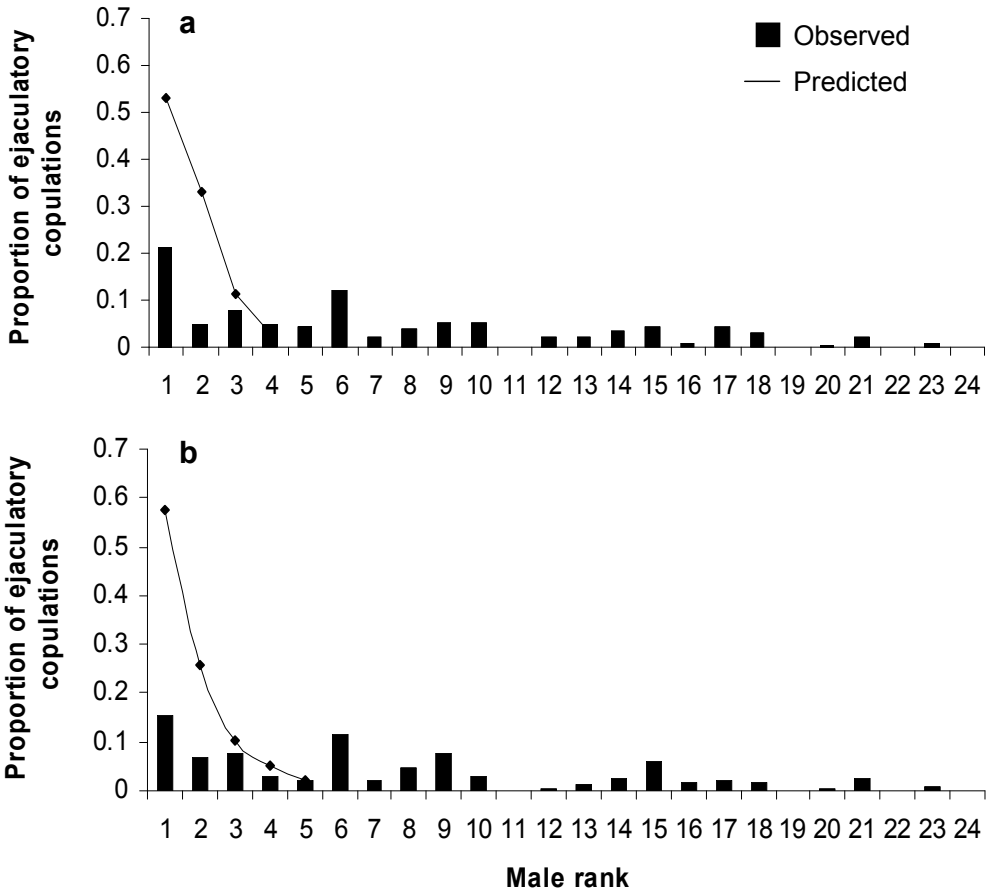


Figure 5-2 Proportion of ejaculatory copulations by males of each rank. Predicted values were calculated from the distribution of female (a) attractive days or (b) peri-ovulatory days during the period ranging from 10 November until 13 February, using the priority-of-access model (see details in text).

The vast majority of consortships obtained by a subordinate male challenger from a dominant rival occurred through coalitionary changeovers (19/83, i.e. 23%) or avoidance (34/83, i.e. 41%). Coalitionary changeovers occurred when two subordinate, post-prime males directed a successful coalitionary attack against a dominant, prime male who was consorting a female or attempting doing so (12 cases), or when a prime male retreated from a female or let his female partner go as a response to the threat of a coalitionary attack (7 cases; see the operational definition in the Methods section). The dominant coalition partner formed a new consortship and/or mated with the contested female after most (8/12) of the successful coalitions, although the subordinate partner sometimes obtained priority-of-access (subordinate: 3 cases; both partners sequentially: 1 case).

The finding that dominant males often lost a female through avoidance of a subordinate male challenger was unexpected. A closer a look at the data revealed that in almost 60% (20/34) of the cases a prime male avoided a subordinate challenger,

who was a post-prime male. In all 20 cases the post-prime male challenger had already formed a coalition against the prime male earlier in the mating season. It has already been reported that the response of Barbary macaque males to the threat of a coalitionary attack could be subtle, so that a prime male could already retreat from a female if only one older male appeared (Kuester and Paul 1992). If we accept the possibility that prime males may have forgone mating opportunities in response to the potential threat of a coalitionary attack by a subordinate post-prime male, it would increase the proportion of changeover related to coalitionary activity to 47% (and decrease that of avoidance to 16.7%). Of the 14 remaining cases of avoidance by a dominant individual, 13 occurred when a dominant post-prime or prime male lost his consort to a subordinate prime male, and 1 occurred in a dyad of post-prime males.

The frequency of the tactics used by dominant male challengers to acquire consortships from subordinate rivals (i.e. "up the hierarchy") was strikingly different from the picture presented above (Fig. 5-3). The vast majority of the cases (70/110) occurred though avoidance by the subordinate rival. Only 10 instances of overt aggression and 2 cases of escalation to a fight were observed.

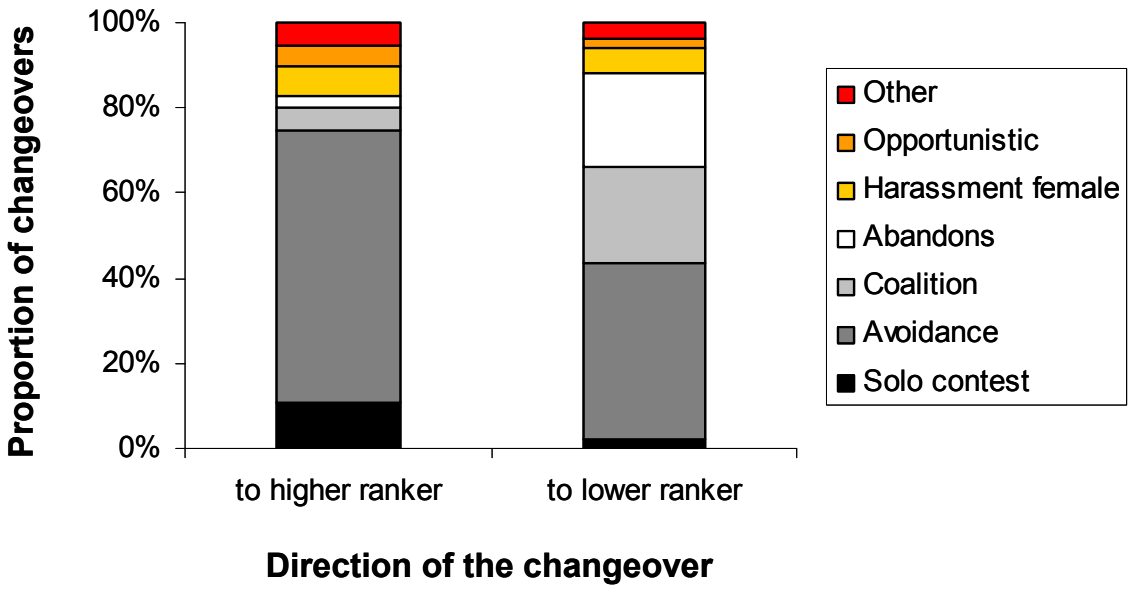


Figure 5-3 Types of changeovers in consortships. To higher ranker: the male challenger was dominant to the previous male partner; to lower ranker: the male challenger was subordinate to the previous male partner (*N*=193). A large proportion of the changeovers going to a lower ranker and classified as "avoidance" may rather belong to the category "coalition". If we accept this interpretation, it would increase the proportion of changeover related to coalitionary activity to 47% (and decrease that of avoidance to 16.7%, see explanations in text).

Behavioral mechanisms decreasing skew: the female perspective

Females in our study showed a promiscuous mating pattern: attractive and peri-ovulatory females performed ejaculatory copulations with 1 to 13 males per cycle (mean attractive female: 7.3; mean peri-ovulatory female: 5.4). To determine to what extent females actively sought out multiple males, we looked at how active females were in initiating their consortships and how they distributed their initiations over males of different dominance rank or age. The analyses were performed for females on their attractive and peri-ovulatory days, but because very similar results were obtained for both data sets (unpublished results), we only present the analyses of 221 changeovers with attractive females for which the initiator of the new consortship could be identified (mean number of consortship per female: 20.6; range: 3-63).

Our data show that similar proportions of consortships were initiated by females and males (females: 121; males: 102; both: 2), with individual females establishing on average 43.3 % (range 0%-83.3%) of their consortships themselves. On average, during observation times, attractive females initiated consortships with 5.1 (range 1-11) different partners.

Logistic regression revealed that females were more likely to initiate consortships with younger than older males, but did so independently of male rank (Table 5-2). Indeed, 69.4% (84/121) of the female-initiated consortships where directed towards prime males, and in most of the cases (54/84) females visited them up in a tree (see Chapter 4). Most of the consortships formed by prime males were initiated by females (84/105), suggesting that prime males strongly relied on females to acquire mating opportunities. This is in sharp contrast with older males, who themselves initiated most of their consortships (37/116 initiated by females; Chi-square test: $\chi^2 = 51.48(1)$, $P< 0.0001$; Fig. 5-4). Because females preferentially initiated their consortships with prime males, who generally (but not always) occupied higher rank than the previous male partner, females were also more likely to initiate consortships with dominant challengers (dominant challenger: 58.2%; subordinate challenger: 34.1%; Chi-square goodness-of-fit: $\chi^2 = 7.09(1)$, $P= 0.008$).

Table 5-2 Independent variables predicting the likelihood of females responsibility in initiating consortships in a logistic regression analysis (*N*= 223 consortships).

Independent variable	Regression coefficient	SE	z	*P*
Univariate analyses				
Male age	-0.2	0.04	-4.45	**<0.0001**
Male rank	-0.07	0.05	-1.46	0.143
Bivariate analyses				
Male age	-0.23	0.05	-3.97	**< 0.0001**
Male rank	0.03	0.04	0.67	0.502

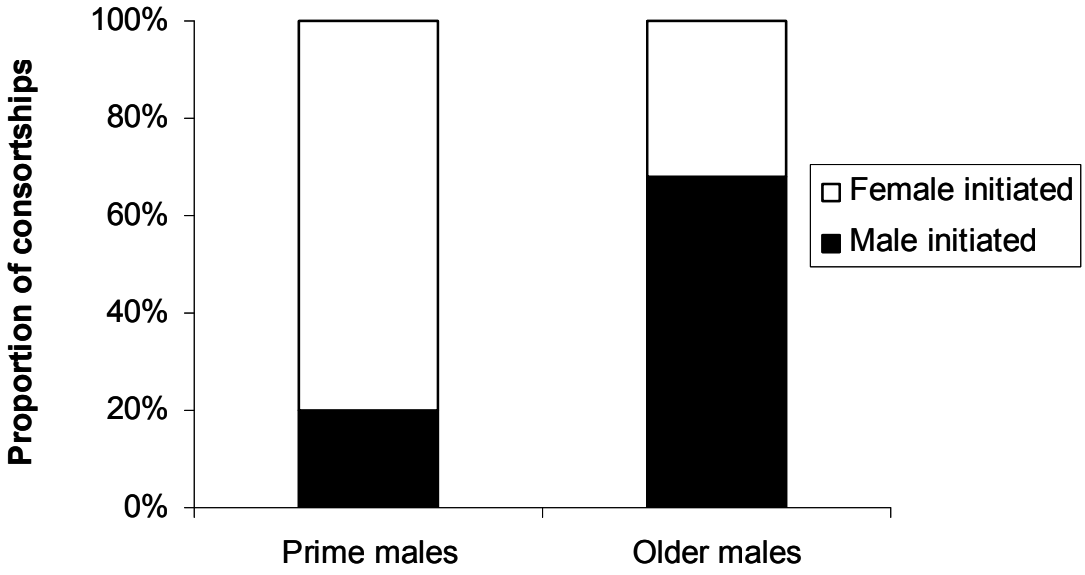


Figure 5-4 Proportion of consortships initiated by males and females according to male age class.

Discussion

Our data confirm the findings of a number of authors, that a low to medium skew is a constant characteristic of Barbary macaque males (cf. Table 5-3; one exception in a small group with 1-2 adult males: Witt et al. 1981). By providing a first test of the PoA model in this species, we could show that female cycle overlap sets an upper limit to the monopolization potential of dominant males, as would be expected in a seasonally breeding species (Cowlishaw and Dunbar, 1991; Paul, 1997), but this factor alone was not sufficient to explain the distribution of matings among male ranks (see below). Our results, together with those of other studies (cf. Table 5-3), suggest that there are some benefits associated with a high-rank for a Barbary macaque male, although that are relatively low in comparison to other non-seasonally breeding species (e.g. chacma baboons: Weingrill et al., 2003; mandrills: Setchell et al., 2005; long-tailed macaques: Engelhardt et al., 2006). Overt aggression over access to females was rarely seen and the rank effect was mainly brought about by the active avoidance of dominant male challengers by subordinate males (Fig. 5-3). However, given that age and rank are closely related in the Barbary macaque (Paul 1989; Brauch et al. 2008; this study), as in other macaque species (reviewed in Sprague, 1998), these two effects cannot easily be disentangled. Some authors concluded that male-male competition was simply absent in Barbary macaques and thus argued for a strong scramble component (sensu Nicholson, 1954) to mating competition (Taub, 1980; Small, 1990). However, current evidence (Witt et al. 1981; Kuester and Paul 1992; Brauch et al. 2008; this study) shows the clear presence of a contest component to mating competition in this species. The finding that Barbary macaque immigrants prefer groups with fewer males of their age than in the natal group (Kuester and Paul, 1999) further suggests that the prospect of contest competition influences males' career decision in important ways (van Noordwijk and van Schaik, 2001).

Leveling coalitions

The presence of a stable hierarchy is a prerequisite to an association between rank and mating success, but the degree to which a high rank may confer benefits to males appears to be at least partly contingent upon the frequency and efficiency of male coalitions. Kuester and Paul (1992) concluded that power asymmetry among Barbary macaque males is not always determined in the "classical" one-to-one fashion. In line with these findings, we have shown that coalitionary activity can have an important impact on male mating success and efficiently decreases skew among males, as shown in savanna baboons (Bercovitch, 1988; Noë and Sluijter, 1990; Noë, 1992; Alberts et al., 2003), although between-group variation in the frequency of this

behavior linked to the cohort size of post-prime males is found (Alberts et al. 2003; this study, Chapter 4).

In the current study, mostly post-prime, subordinate males used the coalitionary tactic to level mating access by targeting a consorting male or preventing the target from establishing a consortship at all. Overall, all-up, leveling coalitions accounted for an important proportion (23%) of changeovers from a dominant male to a subordinate challenger, and thus played an important role in decreasing mating skew. However, we think that this figure may only represent a conservative estimate of the impact of coalitionary activity on mating skew. Indeed, if we accept the possibility that prime males sometimes forwent mating opportunities by avoiding subordinate, post-prime males who formed coalitions against them in the past, as suggested by others (Kuester and Paul 1992), the proportion of changeovers related to coalitionary activity reaches 47%.

Barbary macaques appear to differ from other macaque species, where coalitions are mostly used by males to stabilize the existing hierarchy (e.g. Tibetan macaques: Berman et al. 2007; Assamese macaques: Ostner et al. 2008). This difference may be linked to a difference in the level of mating competition among males as suggested by van Schaik and colleagues (2003; 2004; 2006), but the issue of inter-species variation will be treated in greater depth in a future work (A. Bissonnette, O. Schülke and J. Ostner, in prep.).

Promiscuous or "choosy" females?

In line with previous studies, we found that Barbary macaque females play an active role in initiating their consortships, seek multiple males during their attractive and peri-ovulatory periods, and are cooperative with most partners (Taub 1980; Small 1990; Kuester and Paul 1992; Brauch et al. 2008; own obs.). Taken together, these results suggest that Barbary macaque females are pursuing a promiscuous mating tactic, as observed in many other primate species (e.g. Hrdy, 2000; Paul, 2002; Nikitopoulos et al., 2005). Among the potential benefits of promiscuous mating would be avoiding inbreeding or genetic incompatibilities (e.g. Zeh and Zeh, 2001), allowing sperm from various males the chance to compete for fertilization (e.g. Dixson, 1998; Brauch et al., 2008) and reducing the risk of infanticide (e.g. Hrdy, 1979; van Schaik et al., 2004b).

Yet, we also found evidence that females were more likely to initiate their consortships with prime males by visiting them in the trees, which suggests that females were exerting mate choice based on an age criterion. Selective and promiscuous mating may not necessarily be mutually exclusive mating patterns, for example if females mate with multiple males, yet copulate more often with certain males compared with others (i.e. "discriminative mating", cf. Nikitopoulos et al., 2005). However, this result is puzzling, because this preference for prime males does

not appear to be common in primates (Small, 1990; Paul, 2002; Soltis, 2004) and has never been reported to date in Barbary macaques.

We think that the clear female preference for prime males in the current study may reflect the unusually large number of post-prime males in this group, which enables the post-prime cohort to effectively peripheralize the prime males (see Chapter 4). As a consequence, females may have used different tactics to achieve copulations with males of different age class, i.e. they may have actively approached prime males as a part of a promiscuous tactic which aims at equalizing matings among males (for a similar argument in rhesus macaques see Manson, 1992). However, to fully resolve this question an experimental set-up would be needed where female have complete control over access to males of different age and rank (see Nikitopoulos et al., 2005 for an example in long-tailed macaques). This was unfortunately outside the scope of this study.

Irrespective of their underlying strategy, females in the study group contributed to reinforce mating skew by preferentially initiating their consortships with prime males, who generally (but not always) occupied higher rank than the previous male partner, thus impeding post-prime males to accumulate a disproportionate share of the matings. Thus, this study provides a clear example of how the observed skew among males can be a comprise between male and female efforts (see also Manson, 1992; Soltis et al., 2001).

Limited control or concession?

What can our data tell us about which model of reproductive skew best fit Barbary macaques? The observation in the study group that female cycles overlap to a certain extent and that male-male coalitions can effectively decrease mating skew (Table 5-3; this study) provide convincing support for the limited control model (Cant, 1998; Clutton-Brock, 1998; Reeve et al., 1998). Moreover, the continuous presence of attractive/ peri-ovulatory females, which is common in Barbary macaque groups (Kuester and Paul, 1984, Fig 2; Small, 1990, Fig. 1; this study), may reduce the monopolization potential of dominant males because consorting is costly to males in terms of time, energy and opportunity costs (Kutsukake and Nunn, 2008; Ostner et al., 2008b). For example, the observation that the alpha male in our study group completely monopolized the beta female during 36 days at the beginning of the mating season, but did not show other monopolization cycles afterwards despite its ability to do so, may suggest that consorting females involve costs and thus limit the number of days a male is able to consort. However, further studies will be needed to identify the exact nature of the costs of mate guarding (if any) in Barbary macaque males.

In conclusion, it appears more likely that like other primates dominant Barbary macaque males have a limited control over reproduction (see also Brauch et al., 2008). On the one hand, our findings show that the ability of dominant males to

monopolize females is limited by female cycle synchrony, in line with the PoA model. On the other hand, strong deviations from the predictions of the PoA model suggest that in addition to female synchrony, male-male coalitions and to a lesser extent female promiscuous behavior limit monopoly by dominant individuals. However, the relative importance coalition formation in producing deviations from the PoA model is contingent upon the cohort of post-prime males, as suggested in savanna baboons (Alberts et al., 2003). Clearly comparisons of groups of different age composition are needed for a better understanding of the factors influencing male mating success in Barbary macaque males.

Table 5-3 Principal results of field studies of reproductive success in Barbary macaques

Study[1]	Living conditions	# adult males[2]	Measure of reproductive success	Prop of mating or infants sired by alpha[3]	Correlation rank/ measure of success	Male-male coalitions	Female behavior	Female cycle synchrony
1	Wild	7	Ejaculatory copulations during maximum sexual swelling of females	0.24	high > low rankers	rare over consorts	promiscuous	?
2	Provisioned	11-12	Genetic paternity markers	~ 0.25	No	?	?	?
3	Provisioned	5-12	Genetic paternity markers	0.06 [0 - 0.11]	No	?	?	?
4	Provisioned	4-6[2]	Ejaculatory copulations during the fertile period and genetic paternity markers	?	high > low rankers	?	preference for higher-rankers	30% overlap in fertile days
5,6	Semi-free ranging	5-9	Ejaculatory copulations during the conceptional week	0.29 [0.20-0.38]	yes in 1 of 2 mating seasons	?	?	$\bar{x}$: 2.9- 3.1 fertile females/day in Nov.
7	Semi-free ranging	16-33[2]	Genetic paternity markers	~ 0.16	no[4]	yes	?	?
8	Semi-free ranging	25	Ejaculatory copulations during the conceptional week	≤ 0.13	no?[5]	yes	promiscuous	4-21 females sexually active
9	Semi-free ranging	11	Copulations during maximum sexual swelling of females	?	?	?	promiscuous	58% infants conceived in one month
10	Captive	1-2	Genetic paternity markers	0.69 [0.46- 100]	(only 1-2 males)	yes	?	?

[1] 1.Taub (1980); 2. Kümmerli and Martin (2005); 3. Modolo and Martin (2008); 4. Brauch et al. (2008); 5. Paul (1989); 6. Paul et al. (1993); 7. Paul and Kuester (1996); 8. Paul and Kuester (1992); 9. Small (1990); 10. Witt et al. (1981)

[2]Adult males are ≥ 7 y.o. except for the following studies: Brauch et al. (2008): ≥ 5 y.o.; Paul et al. (1993) and Paul and Kuester (1996): mature males ≥ 4.5 y.o.

[3]The mean proportion per group/year is given for studies with more than one breeding season and the range is shown in brackets when available

[4]Correlation is significant if the sub-adult males (sexually mature but not yet full adult body size) are included.

[5]The low number of agonistic interactions did not allow the construction of a dominance hierarchy.

Chapter 6

Discussion and perspectives

Evaluating a model for male-male coalitions

The recently proposed model on male-male coalitions is an evolutionary model, which assumes that long-term exposure to a limited range of ecological conditions had led to male strategies that produce the best average fitness return in these conditions (cf. Sterck et al. 1997). It states that the occurrence and type of coalitions observed within multi-male groups is determined by the level of sexual contest competition males experience (i.e. β parameter, Pandit and van Schaik, 2003; van Schaik et al., 2004, 2006). Till date the model remained largely untested. A preliminary review of the empirical patterns of male-male coalitions among primates confirmed the strong predictions of the model, although some discrepancies were also found (van Schaik et al. 2004; see below). An important limitation of such literature surveys is that coalitions are often reported in the framework of studies on another topic and important details such as information on the outcome of coalitions (i.e. changing dominance rank, acquiring access to a receptive female or intimidating higher-rankers) is often not reported (e.g. Koyama, 1967). In extreme cases, different interpretations may be possible even when the outcome of coalitions is reported. For example, a study by Witt et al. (1981) in a small group of Barbary macaques is often cited as an example of all-up, rank-changing coalition (e.g. van Schaik et al., 2004; Berman et al., 2007). However, a closer look at the description provided by the authors revealed that "the beta and the gamma male together often managed to exclude the alpha male from contact with estrous females" (p. 205) before the alpha male was deposed, and only the beta male increased in rank after what appeared to be a dyadic fight. It is therefore unclear whether these coalitions may be best interpreted as all-up, (partial) rank-changing or all-up, leveling. It also raises the question whether these two types of coalitions are perceived differently from the animal point of view, but this is an issue that we will not discuss at length here. So far, there only

exists another published study that tests the model (Jones 2005). The author used observational data on male-male coalitions in mantled howler monkeys to test the internal consistency of the model, and concluded that the observed coalition types fit the categories of the model (Jones 2005). Here, we use our data on Barbary macaques to verify whether the most frequent type of coalitions observed in the study group is linked with the proposed level of monopolization potential, and discuss some limitations and possible extensions of the coalition model.

A case-study: the Barbary macaque

To test the predictions of the coalition model with real systems, it is crucial to estimate the model's main parameter β. In permanent, mixed-sex groups, its value is mainly determined by the degree of overlap in female estrous cycles (which is in turn determined by the number of females in the group, the degree of reproductive seasonality, and female reproductive physiology, such as length of the attractive period, the number of cycles per conception and the presence of 'cycles' during pregnancy, cf. Altmann 1962), and female behavior in terms of preferences for mating with dominant or subordinate males, or for polyandrous mating (van Schaik et al. 2006; Fig. 6-1). van Schaik and colleagues (2004) used the observed paternity or mating success of the top-ranking male as an estimate of the monopolization potential (i.e. $\beta_{observed}$, Fig. 6-1), which should constitute a good estimate of β in the absence of leveling coalitions. However, $\beta_{observed}$ will underestimate monopolization potential in species where leveling coalitions are common, because it constitutes a post-hoc estimate after coalitions. In this situation, one alternative is to use the priority-of-access model (cf. Altmann, 1962) to set the basic expectation of monopolization potential among males (i.e. β_{poa}, Fig. 6-1), given that detailed information on female cycle overlap is available (see Chapter 5). β_{poa} gives an estimate of monopolization potential before coalitions, but will overestimate the actual monopolization potential in species where females actively act to reduce monopolization by dominant males (see references in Chapter 5; note that the use of proxies for female synchrony (Nunn, 1999) would also show the same tendency to overestimate monopolization potential). The issue how to estimate monopolization potential in a way that will not suffer from these limitations and be generalizable across species is currently under investigation (A. Bissonnette, O. Schülke and J. Ostner, in prep.), but for now the most appropriate solution would be to use β_{poa} as an upper limit and $\beta_{observed}$ as a lower limit to male monopolization potential. The estimate of β for the Salem group ranges between 0.21 ($\beta_{observed}$) and 0.52 (β_{poa}), based on the proportion of ejaculatory matings by the alpha male with attractive females (Chapter 5).

In the Salem study group, all-up coalitions were the most frequent type of coalitions observed (72%), although other coalition configurations also occurred. We found evidence for a leveling function of all-up coalitions: (1) coalitions were mostly formed by males ranking well below the top and with little prospect of attaining that position, (3) they involved various combinations of lower-raking males/higher-

ranking targets (in contrast to rank-changing coalitions which are expected to be repeatedly formed by the same two high-ranking partners and targeted at a single male, almost always the top-ranking one), (3) they occurred during the mating season, and (4) had a positive impact on the mating success of lower-rankers, although females were also shown to reduce the efficacy of this tactic (Chapter 5). Most interestingly perhaps, we observed that an important part of the coalitions occurred in the absence of any direct competition for females, and presented evidence suggesting that coalitions may be used to level mating access by intimidating higher-ranking, prime males in showing restraint in mating competition (Chapter 4).

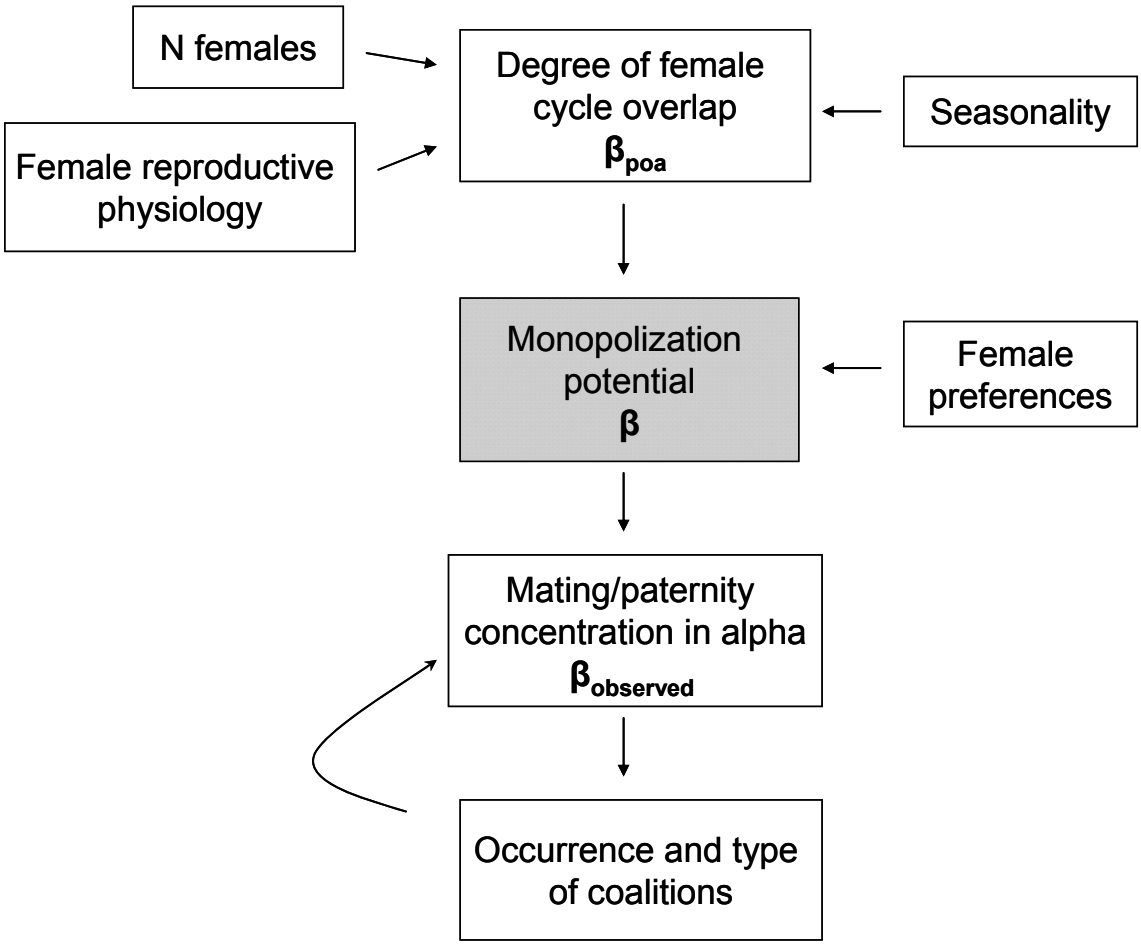


Figure 6-1 Factors influencing monopolization potential (β) in primates and different levels at which it can be estimated (modified from van Noordwijk and van Schaik, 2004a, fig. 12.1).

In sum, the results of this study largely support the prediction of the coalition model that all-up, leveling coalitions occur at low-medium monopolization levels

(Table 1-1). All-up leveling coalitions were also reported in another group of Barbary macaques of the same population at low monopolization potential (βobserved ≤ 0.12, Kuester and Paul, 1992; but see Witt et al., 1981). Given that species-specific characteristics such as a seasonal breeding and a promiscuous mating system usually translate into a relatively low potential for male monopolization in natural groups of Barbary macaques (Chapter 5), we may expect these findings to be replicated in other populations of the same species, perhaps contingent on the cohort size of post-prime males (see below).

Limitations and possible extensions of the current approach

Not all aspects of male-male coalitions reported in this and other studies fit the predictions of the model. We discuss two here: the strong age-related expression in coalitionary activity and the smaller than expected size of leveling coalitions.

Demography as a possible constraint on coalition formation

The finding that prime males in our study group rarely participated in coalition formation, together with the observation that coalitions were rare or absent in at least two multi-male group of Barbary macaques with only one post-prime male (K. Brauch, pers. comm.; Wildpark Daun, own obs.) suggests that age act as an important constraint on the expression of coalitions in Barbary macaques, a factor that is not considered in the coalition model. Similar age effects are seen in savanna baboons (Bercovitch, 1988; Smuts, 1985; Noë, 1992; Alberts et al., 2003), although the age rule appears to be less stringent in baboons that Barbary macaques (see Table 11.1 in Noë, 1992). In Chapter 4, we proposed three as yet untested, non-mutually exclusive hypotheses to explain why prime males rarely or never participate in coalitions. All three hypotheses suggest that the costs of coalitions vary in relation to age, so that at constant rank coalitions are less profitable for younger than older males. This possibility is not considered in the coalition model, which assumed that at constant contest level payoffs are equal for males of equal rank, irrespective of their age. By introducing costs in the coalition model that vary as a function of age, subadult and prime males would obtain lower payoffs and be less likely than post-prime males to participate in coalitionary activity, thus explaining the age-related pattern in coalition formation.

More tests in different species will be needed to determine whether this age-related pattern is common among primates or only observed in a handful of species, but it is clear that the demographic structure of a group now becomes an issue to be examined both empirically and theoretically.

Constraint on coalition size?

The model predicts that leveling coalitions will be large and consist of mid to lower rankers (Table 1-1). However, it failed to correctly predict the small size of leveling coalitions in savanna baboons (Fig. 2 in Pandit & van Schaik 2003) and in Barbary macaques (Kuester and Paul 1992; this study). There are many potential theoretical and biological reasons for this discrepancy, discussed at length by van Schaik et al. (2006). However, the proposed biological reason that larger coalitions do not form because males may have trouble finding suitable partners (van Schaik et al. 2006) is unlikely in the present case, because the group was composed of an unusually large cohort of post-prime males who frequently participated in coalition formation. Another possible explanation for the smaller than expected coalition size is that the prize, i.e. access to the female, can only be shared statistically and it may represent a cognitive challenge for males in larger coalitions to keep track of their average payoff (Pandit & van Schaik 2003). However, this constraint is also unlikely to apply for coalitions aimed at intimidating higher rankers in the absence of any direct competition over females. These coalitions were of small size in the study group. At this stage, we cannot provide any firm answer as to why leveling coalitions, and most within-group coalitions, among primates are limited in size (reviewed in van Schaik et al. 2004), but the presence of this constraint on coalition size is an issue that needs to be examined in future work.

Conclusions and future work

Given the indirect nature of most previous testing, the results of the predicted link between the level of monopolization potential and male-male coalition types remain preliminary. Current evidence suggests that the coalition model has some heuristic value in Barbary macaques, but as this study shows, additional factors such as the age constraint on coalition formation may also need to be incorporated. Once data become available for more species, it will be possible to test the overall validity of the model and expand or modify it if required. This constitutes one important goal of ongoing comparative work (A.B., O. Schülke, J. Ostner, in prep.).

At this point, it is important to stress that the coalition model is a cost-benefit model that focuses on conditions in which coalitions are successful and profitable. As such, it is not concerned with the actual decision rules and assessment mechanisms that are used by the animals. This point was illustrated in Chapter 3, by showing that males do not estimate the asymmetry in strength per se as modeled, but most likely used simple rules of thumb based on knowledge readily available to them. Most models mentioned in the introduction also suffer from this shortcoming (e.g. Dugatkin, 1998, 2002; Mesterton-Gibbons and Sherratt, 2007).

In addition, in this kind of economic analysis there is nothing special about how cooperation is expressed in behavior (Schuster and Perelberg, 2004). For example, an important aspect that is not taken into account by the coalition model is the process of communication between partners. To look at the process of communication could be helpful to infer whether the actions are intentionally or indirectly directed towards the same goal by the individuals: are the partners truly cooperating or working apart together (Noë, 2006; Chalmeau and Gallo, 1996)? A number of primate species report the use of "side-directed behavior" (cf. de Waal et al., 1976) before and during coalitions (de Waal 1982; Smuts & Watanabe 1990; Noë 1992; this study: silent-scream face, Fig. 4-2). Such behavior is thought to contain a proposal to form a coalition, or to continue and ongoing interaction (Noë, 1992), thus suggesting that the individuals often are aware that their partner(s) is instrumental in achieving a goal. Another important aspect is the stability of coalitions. Coalitions can be variable in their composition, i.e. they can occur opportunistically on a case-by-case basis, or represent long-term alliances (e.g. Noë, 1986; Goodall, 1986; Smuts, 1985; de Waal, 1982). It has been suggested that the stability of coalitions may be a function of the number of possible alternative combinations that can be formed by either ally, or a consequence of the costs involved in a change of partners (Noë, 1989, p. 218). Preliminary results suggest that males in the Salem group formed coalitions in an opportunistic, case-by-case basis rather than alliances (Fig. 6-2). The various aspects of coalition dynamics in Barbary macaques will constitute an important focus of future work. To conclude, a careful empirical investigation of both the proximate mechanisms and the ultimate consequences is a necessary step towards a complete theory of coalition formation in animals.

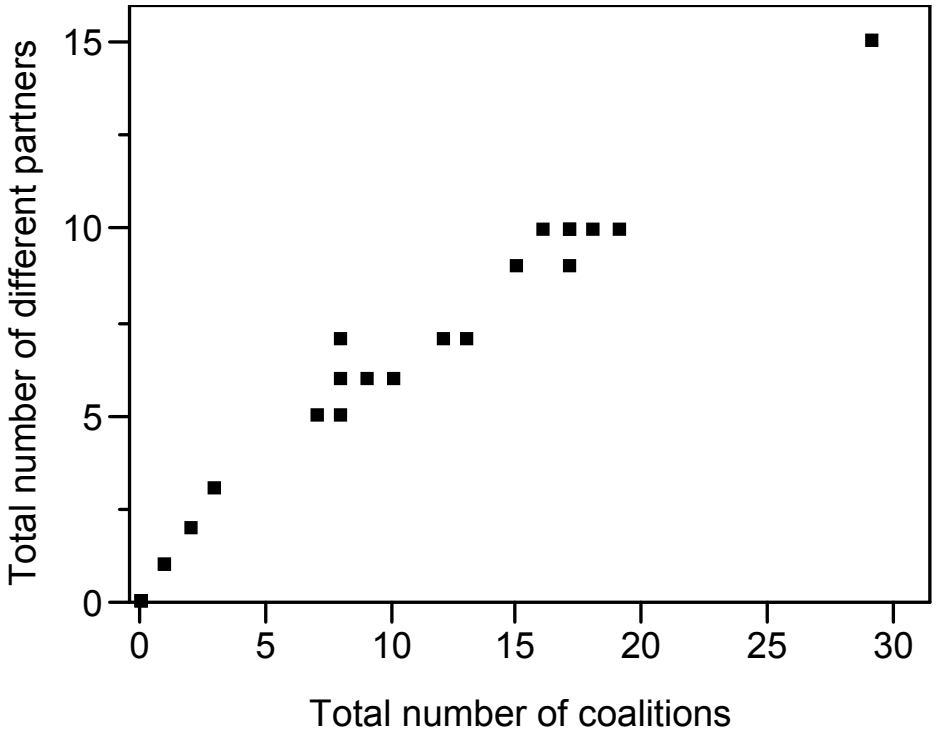


Figure 6-2 In the Salem group, the more coalitions a male formed the more partners he had (r= 0.98, p<0.0001, *N*=20), which suggests that coalitions were mostly formed on a case-by-case basis.

Appendix A

Complete name, shortcut and tattoo of the adult animals present in the Salem group H during the mating season 2006/07*

Male Name	Shortcut	Tattoo	Female Name	Shortcut	Tattoo
Eyebrow	Eyb	Y2	Omi	Omi	U1
Charles	Cha	Z30	Butterfly	But	A57
Bernard	Ber	C5	Alias	Ala	A62
Lucky	Luc	C13	Ducky	Duc	A76
Penny	Pen	D10	Eyeless	Eyl	B87
Techniker	Tec	D11	The beast	Bea	B89
Pig nose	Pig	D13	Apple	App	B91
Watermelon	wme	D25	Dirty	Dir	C73
Hulk	Hul	D27	Bonny	Bon	D50
Fu-guy	Fug	D29	Stella	Ste	D52
Frodo	Fro	E13	Hera	Her	D55
Funny lips	Fun	E14	White stripe	Whs	E52
Flappy nose	Fln	F3	Madonna	man	E58
Silas	Sil	G4	Janis	Jan	F64
Punky	Pun	H3	Fetkeks	Fet	F68
Bello	Blo	I2	Mado	mad	G52
Yaku	Yak	J3	Blue	Blu	G60
Ludwig	Lud	L1	Fanny	Fan	I50
Ronny	Ron	M1	Bella	Bel	I52
Wart	War	N1	Colliflower	Col	I55
Leon	Leo	N2	Lola	Lol	L51
Neo	Neo	O2	Ali	Ali	N53
Flint	Fli	O3	Slappy	Sla	P50
Johnny	Joh	Q7	Missy-2-dots	M2d	Q53
			Triangle	Tri	R50
			Mum	Mum	R53
			Hübsche	Hub	S51

*Additional information on male rank, age and natal status is given in Table 4-1, and on female rank, age, parity and implantation status in Table 5-1.

Complete name, tattoo and age of the adult animals present in the Daun group during the mating season 2005/06

Male Name	Tattoo	Age	Female Name	Tattoo	Age
Leolo	Gi 5	15	Monika	Gi 2	22
Lollipop	RH 1	10	Raisin	Gi 4	21
Sansibar	RH 3	10	Judith	Gi 6	18
Sarotti	RH 9	10	Diana	Gi 8	13
Flint	RH 5	9	Linchen	Gi 10	13
Silas	RH 7	9	Baba	Gi 12	13
Charles	Gi 11	8	Josephine	Gi 14	12
Roger	Gi 17	7	Victoria	Gi 16	9
			Elisabeth	Gi 18	9
			Sina	RH 6	9
			Doris	Gi 22	7
			Leila	RH 6	7
			Jana	Gi 30	7
			Antje	DA 2	6
			Bianca	DB 4	5
			Bella	DB 2	5

Appendix B

Ethogram of *Macaca sylvanus* used during this study*

Shortcut	Definition of behavioral patterns
Agonistic behavior	
sta	Stare: The mouth is closed or slightly open with the lips concealing the teeth and eyebrows are raised revealing the paler skin above the eye. The eyes are wide-open and the ears are sometimes flattened towards the head.
omf	Open-mouthed face: Mouth open with the lips usually concealing the teeth.
lun	Lunge: The subject lunges toward the object briefly.
cha	Chase: The subject chases the object for more than 2 meters (otherwise "lunge").
sla	Slap: The subject hits the object with the hand, i.e. there is a physical contact.
sla-w	Slap without contact: The subject hits in the direction of the object without touching him.
pus	Push: The subject pushes the object with the hands.
gra	Grab: The subject seizes the object's fur with the hands.
inhbit	Inhibited biting: Placing one's open mouth on the partner without closing it or softly biting the body part of another individual, inducing no apparent reaction or a weak reaction (e.g. look at) in the target. Usually displayed together with an affiliative behavior (e.g. mounting, embracing).
bit	Bite: Biting another individual, inducing jumping or moving away suddenly (i.e. startle reaction) or counter-attacking in it.
grow	Growl: Call given when threatening and attacking (and also at predators).
avs	Avoid staring at: Subject glances away from the object, in response to a threat or aggression received.
lat	Look apprehensively towards: Subject gives furtive or "nervous" glances towards the object.
grin	Silent bared-teeth display (fear grin): The lips are withdrawn to reveal both rows of teeth. Given in response to aggression or as a spontaneous submissive signal.
ima	Intention movement away from: Standing or sitting subject leant away from object sometimes lifting a forelimb from the ground or standing if previously seated.
wa	Walk away: The object leaves its place when the subject passes by, walks towards or looks at it, or in response to any action.
flee	Flee: The subject leaves rapidly the object, for example after an aggression received.
cro	Crouch: Subject flexes its limbs so that its body is lowered towards the ground. Can be given by a monkey in response to a threatening gesture, chase or attack. (Behavioural pattern also observed in non-agonistic contexts).
scr	Screams: Calls given in response to threat or attack. Can also be given in the absence of aggression to enlist the support of other individuals. (submissve - protest- and/or sollicitation)
scr-short	Short screams: Calls given in response to threat or attack but of lower intensity and shorter duration than the screams.

Shortcut	Definition of behavioral patterns
chat	Chatters: Short, sharp units that are given in response to a threat (sounds a little bit like a duck). Can also occur in non-agonistic contexts (see below).
fo	Face object: The subject being target of an aggression stops running away from the object and stands facing it.
f-to-f	Face-to-face: Two animals involved in an aggression are standing or sitting facing each other, generally showing a scream face or screaming.
bf	Back and forth: The subject lunges towards and backs away from the object during an agonistic encounter. This behavioral pattern can be interpreted as a sign of contestation from the animal being the first target of aggression.
Agonistic behavior specific to polyadic interactions	
scrf	Silent scream face: Mouth wide open, lips completely retracted so showing the teeth. Prolonged glances can be made at other individuals and this sometimes has the result of enlisting them to form a coalition against a threatener (see head-flagging and look around). SILENT.
hfl	Head-flagging: The object looks alternatively from an individual that he is threatening or receiving aggression from, to another individual to enlist its support. Generally accompanied by screaming or a silent scream face.
look-a	Look around: One or more animals involved in a conflict look around, generally screaming or showing a scream face. In contrast to head flagging, this behavior is not directed at a specific individual, but can be interpreted as "looking around for help".
stand //	Stand parallel: Two or more animals stand parallel shoulder to shoulder and face a common target.
stand-b	Stand behind: Used when one or more animals stand close behind the recipient or the aggressor or the victim of an aggression i.e. within 5 meters
att	Attendance: An animal moves toward a conflict and look at the opponents without participating i.e. does not show any affiliative or agonistic behavior. The animal would often sit down and follow the scene at a distance.
scr-f	Scream-fight: long-lasting and noisy events characterized by two primary antagonists screaming at each other and third parties joining the conflict as a response
coal	Coalition: A joint aggression between at least two individuals against a common target, which occurs outside the context of scream-fights
agg-r	Redirected aggression: An individual threatened or attacked by another shows aggression toward a third individual.
Affiliative behavior	
a	Approach: An individual walks towards and stops within 2 meters of another individual. (It is important to note if the approchee is alone or within 2 meters of any other individual. In this case the third individual could be the actual approchee).
a-s	Simultaneous approach: Two individuals walk toward- and stop within 2 meters of each other simultaneously.
moveclo	Move closer: Subject moves closer to object when already within the 2 meters distance.
incdist	Increase distance: Subject moves away from object, but stay within the 2 meters distance i.e. do not "leave".
lea	Leave: An individual walks from another individual and increases the distance to more than 2 meters.
lea-s	Leave simultaneously: Two animals walk from each other simultaneously and increase the distance to more than 2 meters.

Shortcut	Definition of behavioral patterns
mn	Move near: Subject walks near the object and stops without approaching it directly, i.e. between 2 and 10 meters.
fol-i	Invitation to follow: An individual moves in one direction, sometimes stopping and looking backward toward a partner (e.g. by a female to induce a sexual partner to follow).
fol	Follow: Subject keeps close behind object or moves along some distance behind it (usually along the same route) with its behavior clearly oriented towards the object.
gro	Allogrooming: The subject parts the object's fur with its hands and picks up particles with either fingers or mouth.
gro-m	
gro-sol	Solicitation for allogrooming: Several postures are grouped together. The patterns in the present context are given directly at another individual and appear to be more stereotyped than similar postures given in other circumstances. They include: (i) sitting in front of the object, (ii) sitting upright in front of the object, (iii) laying down on one side, (iv) laying on the ventrum and (v) sitting sideways to the object and bending down in front of it.
gro-stop	Stop grooming: self-explanatory.
grasp	Grasping: Gently grasping any body part of another individual with one or both hands (e.g. rump, hind limbs, arm).
reach	Reach-around: Passing one or both arms, around the body of another individual
emb	Embrace: Embracing another individual ventro-dorsally or face to face. Both individuals are usually seating.
hug	Hugging: Clasping another individual while keeping that animal below oneself; distinct from mounting in that the clasped animal is crouching or sitting.
anti	Antiparallel clicking: Two females stand in body contact and face opposite direction with the arm over the back of the partner and teeth-chatter to the partner's anogenital region.
tria-	Triadic interaction: Two animals are performing an affiliative behavior accompanied by a baby. The affiliative act can vary and must be specified. Ventral-ventral embrace concurrently with teeth-chattering is common
slu	Sit and leg up: The subject sits facing the object and raises its leg, showing its genital organs to the object. Usually accompanied by teeth-chattering.
69	
lip	Lip-smacking: An expression in which the under-jaw is moving up and down rapidly, the lips remain pressed together and slightly rolled inwards.
lip-m	Mutual lip-smacking: Two animals lip-smack mutually.
tcha	Teeth-chattering: The lips are withdrawn to reveal one or both rows of teeth and the lower jaw is moved up and down rapidly.
chat	Chatters: Vocalization given in situation involving babies. Also given in agonistic contexts (see above).
pur	Purring: Series of low sounds given in affiliative situations, e.g. in situation involving babies.
run //	Run parallel: Two or more animals run in parallel. Can occur before or more often after an agonistic interaction.
run // B	Run parallel bump: As above with the two animals bump into each other during the run.

Shortcut	Definition of behavioral patterns
Sexual behavior	
pre/pre-i	Present/Inclined present: Standing stiffly (either in front of or to the side of the object) and with its behind turned towards the object. Often accompanied by looking at the object and sometimes by backing up towards it. (Also observed in non-sexual situations).
hb	Head bob/ head duck: The subject looks at the object and bobs the head up and down. A posture sometimes given by a female to her consort, apparently instead of a presentation. Can also be given in non-sexual contexts.
ins	Inspect: Placing face towards the ano-genital area of a standing or sitting monkey or sitting in front of it and bending down into its groin. Given by the male to the female after an approach by either partner or presentation by the female.
sni	Sniff: Placing the face very close to the ano-genital area of a female.
tou	Touch: Subject touches the sexual swelling or the vulva of the female with its hands.
mgo	Manipulate genital organs: Manipulation of a male genital organs.
ccall	Copulation call (jabbers): Vocalization given by females when copulating.
ecall	Estrous call: Call uttered by estrous females when they are not engaged in any mating activity. Often followed by the male inspecting the female's genitalia and mounting.
pus	Push on shoulder or side: A male approaches a seated female and pushes it with one hand or grips the fur of the female's back and pulls her to her feet. Pattern used by males to get a swollen female to stand, usually followed by examination of her ano-genital area.
how	Hands on waist: Subject, standing or sitting behind standing object, placed its hands on either side of the object's body. Important component or mounting, usually followed by the subject gripping the hind legs of the object.
mount	Mount: The subject climbed onto the object's back to assume the copulation position.
pmf	Post-mount flight: The female runs away some meters from the male partner immediately after dismount.
pt	Pelvic thrusts: Rhythmic dorso-ventral movements of the pelvis by subjects mounted on an object.
wpt	Without pelvic thrust: The subject mounts the object without pelvic thrusts.
sexg	Sexual grabbing While mounted by another animal, the subject reached around towards the mounter's hind leg or ano-genital area.
ejp/sperm	Ejaculatory pause: It is usually difficult to tell whether intromission and ejaculation occurred in copulation. A pause at the end of thrusting or the presence of ejaculate on the female's genitalia can be used to score ejaculation.
intro	Intromission: To be noted if directly observed. High frequency, regular rhythm, and deep amplitude of pelvic thrusts are good indicators of intromission (Kuester & Paul 1984)
mas	Masturbation: Auto-manipulation of one's genital organs with the hand or rubbing of the clitoris against a fixed object.
Other behavioral patterns	
ign	Ignore: The subject sees a gesture directed at it by another monkey (e.g. affiliation, aggression) and makes no apparent response to it.
dns	Does not see: The subject does not see a gesture directed at it by another monkey (e.g. affiliation, aggression) and consequently makes no apparent response to it.
look	Look at: Subject glances at the object or looks at it for longer periods. (Different from "look apprehensively towards").
sea	Search: Subject attempts to find or see another, sometimes by standing on its two hind legs.

Shortcut	Definition of behavioral patterns
sit	Sit by side, sit sideways, sit facing: Subject sits alone or within touching distance of the object.
ct	In contact: Subject and object sit, stand or lay so that they touch each other without performing any of the other behaviour patterns.
stea	Steal: The subject steels an object (e.g. food) out of the object's hands.
feed	Feed: Subject eats any kind of food.
drin	Drink: The subject drinks water.
walk	Walk: Subject walks on the ground or in the trees.
run	Run: Subject increases its speed on the ground or in the trees. (This behavioral category is only used if the subject is not the target or the performer of aggression.)
jump	Jump: Subject jumps in a tree.
cli	Climb: The subject climbs a tree.
desc	Descend: The subject descends a tree.
sle	Sleep: The subject sits or lies on the ground or in a tree with its eyes closed.
def	defecation: Self-explanatory.
aut-gro	Autogrooming: Picking over or brushing aside one's own fur.
scr	Scratching: Using both fore and hind limbs to scratch oneself.
sha	Shake fur: Shaking one's fur like a dog.
yaw	Yawning: self-explanatory.
ly	Lying: self-explanatory.
play	Play: Two or more animals play together, e.g. "chasing game", "restling game", "play with object", etc.
pf	Relaxed open-mouth face (play face): Mouth wide open with the upper lip tight over the upper tooth row (and usually concealing this) and the lower lip slightly retracted revealing the lower teeth. Expression always associated with play.
sha-t	Tree-shaking: A monkey shakes a tree/ cage by bouncing rapidly on it.
star	Startle reaction: A sudden flexing of the limbs and slight lowering of the head given by a standing animal when startled (e.g. in response to a loud noise).
ba	Barks: The alarm call of the species. A call almost unique to the sighting of a predator or potential predator (including human observers).
int-	Intention: Written before any behavior pattern that was not completed.
mb	Missed beginning: When the beginning of an interaction is missed.
o-o-s	Out-of-sight: When the focal animal is out-of-sight.
cli-sol	Clinging solicitation: Postures that are followed by the baby approaching the subject and climbing onto its back or ventrum. For example the subject stands with its behind towards the baby and looks at it over its shoulder, or crouches completely and looks over its shoulder at the baby and teeth-chatters.
cli-d/v	Cling to dorsal/ventral surface: Baby clings to the subject's dorsal/ventral surface.
prct	Prevent contact: Subject prevents the baby from clinging or being in contact, e.g. by turning its back away from it, rolling over or shaking itself. The mother can also prevent a baby from suckling.
onip	On nipple: Baby or infant holds nipple in mouth.
chu	Chups and cheeps: Calls chiefly associated with loss of contact with the mother. Also given when a baby loses a nipple from its mouth.

*Adapted from Deag 1974.

Bibliography

Alberts SC, Watts HE, Altmann J, 2003. Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, Papio cynocephalus. Anim Behav 65:821-840.

Altmann J, 1974. Observational study of behavior - Sampling methods. Behaviour 49:227-267.

Altmann SA, 1962. A field study of sociobiology of rhesus monkeys, *Macaca mulatta* AnnNY AcadSci 102:338-435.

Archer J, 1988. The behavioural biology of aggression. Cambridge: Cambridge University Press.

Arnott G, Elwood RW, 2009. Assessment of fighting ability in animal contests. Anim Behav:in press.

Bercovitch FB, 1987. Reproductive success in male savanna baboons. Behav Ecol Sociobiol 21:163-172.

Bercovitch FB, 1988. Coalitions, cooperation and reproductive tactics among adult male baboons. Anim Behav 36:1198-1209.

Bissonnette A, de Vries H, van Schaik CP, in press. Coalitions in Barbary macaque males: success, strength and rules of thumb. Anim Behav.

Bissonnette A, Lange E, van Schaik CP, 2009. A cardinal measure of competitive ability in Barbary macaque males (*Macaca sylvanus*). Ethology 115:671-681.

Boehm C, 1999. Hierarchy in the forest: the evolution of egalitarian behavior. Cambridge: Harvard University Press.

Boyd R, Silk JB, 1983. A method for assigning cardinal dominance ranks Anim Behav 31:45-58.

Brauch K, Hodges K, Engelhardt A, Fuhrmann K, Shaw E, Heistermann M, 2008. Sex-specific reproductive behaviours and paternity in free-ranging Barbary macaques (*Macaca sylvanus*). Behav Ecol Sociobiol 62:1453-1466.

Chalmeau R, Gallo A, 1996. Cooperation in primates: critical analysis of behavioural criteria. Behavioural Processes 35:101-111.

Chapais B, 1983. Reproductive activity in relation to male dominance and the likelihood of ovulation in rhesus monkeys. BEHAVIORAL ECOLOGY AND SOCIOBIOLOGY:215-228.

Chapais B, 1995. Alliances as a means of competition in primates: Evolutionary, developmental, and cognitive aspects. Am J Phys Anthropol 38:115-136.

Clutton-Brock TH, Albon SD, Gibson RM, Guinness FE, 1979. The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus L*). Anim Behav 27:211-225.

Connor R, Whitehead H, 2005. Alliances II. Rates of encounter during resource utilization: a general model of intrasexual alliance formation in fission-fusion societies. Anim Behav 69:127-132.

Connor RC, Smolker RA, Richards AF, 1992. Dolphin alliances and coalitions. In: Coalitions and alliances in humans and other animals (Harcourt AH, de Waal FBM, eds). New York Oxford University Press; 233-257.

Croxatto HB, 2002. Mechanisms that explain the contraceptive action of progestin implants for women. Contraception 65:21-27.

David HA, 1987. Ranking from unbalanced paired-comparison data. Biometrika 74:432-436.

de Turckheim G, Merz E, 1984. Breeding Barbary macaques in outdoor open enclosures. In: The Barbary macaque: A case study in conservation (Fa JE, ed). New York: Plenum Press; 241-261.

de Vries H, Netto WJ, Hanegraaf PLH, 1993. Matman: A program for the analysis of sociometric matrices and behavioral transition matrices. Behaviour 125:157-175.

de Vries H, Stevens JMG, Vervaecke H, 2006. Measuring and testing the steepness of dominance hierarchies. Anim Behav 71:585-592.

de Waal F, van Hooff J, Netto WJ, 1976. An ethological analysis of types of agonistic interaction in a captive group of Java monkeys (Macaca fascicularis). Primates 17:257-290.

de Waal FBM, 1989. Dominance 'style' and primate social organization. In: Comparative socioecology: the behavioural ecology of humans and other mammals (Standen V, Foley RA, eds). Oxford: Blackwell Scientific Publications; 243-263.

de Waal FBM, Harcourt AH, 1992. Coalitions and alliances: a history of ethological research. In: Coalitions and alliances in humans and other animals (Harcourt AH, De Waal FBM, eds). Oxford: Oxford University Press; 1-19.

Deag JM, 1974. A study of the social behaviour and ecology of the wild Barbary macaque, *Macaca sylvanus L*. (Ph.D. thesis): University of Bristol.

Dixson AF, 1998. Primate sexuality. Oxford: Oxford University Press.

Dugatkin LA, 1998. A model of coalition formation in animals. Proc R Soc Lond Ser B-Biol Sci 265:2121-2125.

Fa JE, 1986. On the ecological status of the Barbary macaque Macaca sylvanus L. in North Morocco: Habitat influences versus human impact. Biological conservation 35 215-258.

Fooden J, 2007. Systematic review of the Barbary macaque, *Macaca sylvanus* (Linnaeus, 1758). Fieldiana: Zoology 113:1-58.

Gamson WA, 1961. An experimental test of a theory of coalition formation. Am Sociol Rev 26:565-573.

Gavrilets S, Duenez-Guzman EA, Vose MD, 2008. Dynamics of alliance formation and the egalitarian revolution. PLoS ONE 3:1-9.

Goodall J, 1986. The chimpanzees of Gombe: patterns of behavior. Cambridge: Harvard University Press.

Harcourt AH, de Waal FBM, 1992. Coalitions and alliances in humans and other animals. Oxford: Oxford University Press.

Heistermann M, Brauch K, Möhle U, Pfefferle D, Dittami J, Hodges K, 2008. Female ovarian cycle phase affects the timing of male sexual activity in free-ranging Barbary macaques (*Macaca sylvanus*) of Gibraltar. Am J Primatol 70:44-53.

Hrdy SB, 1979. Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. EtholSociobiol 1:13–40.

Huntingford FA, Turner AK, 1987. Animal conflict and fighting behaviour. London: Chapman & Hall.

Hutchinson JMC, Gigerenzer G, 2005. Simple heuristics and rules of thumb: Where psychologists and behavioural biologists might meet. Behavioural Processes 69:97-124.

Johnstone RA, 2000. Models of reproductive skew: A review and synthesis (invited article). Ethology 106:5-26.

Johnstone RA, Dugatkin LA, 2000. Coalition formation in animals and the nature of winner and loser effects. Proc R Soc Lond Ser B-Biol Sci 267:17-21.

Kawai M, 1958. On the system of social ranks in a natural troop of Japanese monkey. I: Basic rank and dependent rank. . Primates 1:111-130.

Kokko H, Linstrom J, 1997. Measuring the mating skew. Am Nat 149:794-799.

Koyama N, 1967. On dominance rank and kinship of a wild Japanese monkey troop in Arashiyama. Primates 8:189-216.

Kuester J, Paul A, 1984. Aspects of reproductive behavior in a large group of semi-free living Barbary macaques (*Macaca sylvanus*) Int J Primatol 5:355-355.

Kuester J, Paul A, 1992. Influence of male competition and female mate choice on male mating success in Barbary macaques (Macaca sylvanus) Behaviour 120:192-217.

Kuester J, Paul A, 1999. Male Migration in Barbary Macaques (*Macaca sylvanus*) at Affenberg Salem. Int J Primatol 20:87-106.

Kummer H, 1973. Dominance versus possession: An experiment on hamadryas baboons. In: Symposia of the fourth international congress of primatology, vol 1: precultural primate behavior (Menzel EW, ed). Basel S. Karger; 226-231.

Kutsukake N, Nunn CL, 2008. The causes and consequences of reproductive skew in male primates. In: Reproductive Skew in Vertebrates Proximate and Ultimate Causes (Hager R, Jones C, eds). Cambridge: Cambridge University Press.

Manson JH, 1992. Measuring female choice in Cayo Santiago rhesus macaques. Anim Behav 44:405-416.

Marsh B, 2002. Do animals use heuristics? Journal of Bioeconomics 4:49-56

Martin P, Bateson P, 2000. Measuring behaviour. An introductory guide, 2nd ed. Cambridge: Cambridge University Press.

Maynard Smith J, Parker GA, 1976. Logic of asymmetric contests Anim Behav 24:159-175.

Mesterton-Gibbons M, Sherratt TN, 2007. Coalition formation: a game-theoretic analysis. Behav Ecol 18:277-286.

Neter J, Kutner HM, Nachtsheim CJ, Wasserman W, 1996. Applied linear statistical models, 4th ed. Chicago: Irwin.

Nicholson AJ, 1954. An outline of the dynamics of animal populations. Aust J Zool 2:9-65.

Nishida T, 1979. The social structure of chimpanzees of the Mahale Mountains. In: Pesrpectives on human evolution: the great apes (Hamburg DA, McCown ER, eds). Menlo Park, CA: Benjamin-Cummings; 73-121.

Noë R, 1986. Lasting alliances among adult male savannah baboons. In: Primate ontogeny, cognition and social behaviour (Else JG, Lee PC, eds). Cambridge: Cambridge University Press; 381-392.

Noë R, 1989. Coalition formation among male baboons (Ph.D. thesis). Utrecht: University of Utrecht.

Noë R, 1990. A veto game played by baboons: a challenge to the use of the Prisoner's Dilemma as a paradigm for reciprocity and cooperation. Anim Behav 39:78-90.

Noë R, 1992. Alliance formation among male baboons: shopping for profitable partners. In: Coalitions and alliances in humans and other animals (Harcourt AH, de Waal FBM, eds). New York Oxford University Press; 233-257.

Noë R, 1994. A model of coalition formation among male baboons with fighting ability as the crucial parameter Anim Behav 47:211-213.

Noë R, 2006. Cooperation experiments: coordination through communication versus acting apart together. Anim Behav 71:1-18.

Noë R, Sluijter AA, 1990. Reproductive tactics of male savanna baboons. Behaviour 113:117-170.

Nunn CL, 1999. The number of males in primate social groups: a comparative test of the socioecological model. Behav Ecol Sociobiol 46:1-13.

Packer C, 1977. Reciprocal altruism in *Papio anubis* Nature 265:441-443.

Pandit SA, van Schaik CP, 2003. A model for leveling coalitions among primate males: toward a theory of egalitarianism. Behav Ecol Sociobiol 55:161-168.

Parker GA, 1974. Assessment strategy and evolution of fighting behavior. J Theor Biol 47:223-243.

Parker GA, Rubenstein DI, 1981. Role assessment, reserve strategy, and acquisition of information in asymmetric animal conflicts Anim Behav 29:221-240.

Paul A, 1989. Determinants of male mating success in a large group of Barbary macaques (*Macaca sylvanus*) at Affenberg Salem Primates 30:461-476.

Paul A, 2002. Sexual selection and mate choice. Int J Primatol 23:877-904.

Paul A, Kuester J, 1988. Life-history patterns of Barbary macaques (*Macaca sylvanus*) at Affenberg Salem. In: Ecology and behavior of food-enhanced primate groups (Southwick CH, ed). New York: Alan R. Liss, Inc.; 199-228.

Paul A, Kuester J, Timme A, Arnemann J, 1993. The association between rank, mating effort, and reproductive success in male Barbary macaques (*Macaca sylvanus*). Primates 34:491-502.

Preuschoft S, Paul A, 2000. Dominance, egalitarianism, and stalemate: An experimental approach to male-male competition in Barbary macaques. In: Primate males: causes and consequences of variation in group composition (Kappeler PM, ed). Cambridge: Cambridge University Press; 205-216.

Preuschoft S, Paul A, Kuester J, 1998. Dominance styles of female and male Barbary macaques (Macaca sylvanus). Behaviour 135:731-755.

Preuschoft S, van Schaik CP, 2000. Dominance and Communication. Conflict management in various social settings. In: Natural conflict resolution (Aureli F, de Waal FBM, eds). Berkeley: University of California Press; 77-105.

Quinn GP, Keough MJ, 2002. Experimental design and data analysis for biologists. Cambridge: Cambridge University Press.

Riss DC, Goodall J, 1977. The recent rise to the alpha–rank in a population of free–living chimpanzees. Folia Primatol 27:134-151.

Sapolsky RM, Ray JC, 1989. Styles of dominance and their endocrine correlates among wild olive baboons (*Papio anubis*) Am J Primatol 18:1-13.

Schuster R, Perelberg A, 2004. Why cooperate? An economic perspective is not enough. Behavioural Processes 66:261-277.

Scott JM, Heglund PJ, Morrison ML, 2002. Predicting Species Occurrences: Issues of Accuracy and Scale. Washington: Island Press.

Small MF, 1990. Promiscuity in Barbary macaques (*Macaca sylvanus*). Am J Primatol 20:267-282.

Smuts BB, 1985. Sex and frienship in baboons. New York Aldine.

Smuts BB, 2002. Gestural communication in olive baboons and domestic dogs. In: The Cognitive Animal: Empirical and Theoretical Perspectives on Animal Cognition (Bekoff M, Allen C, Burghardt GM, eds). Cambridge: MIT Press; 482.

Smuts BB, Cheney DL, Seyfarth RM, Wrangham R, Struhsaker TT, 1987. Primate Societies. Chigaco: The University of Chicago Press.

Smuts BB, Watanabe JM, 1990. Social relationships and ritualized greetings in adult male baboons (*Papio cynocephalus anubis*). Int J Primatol 11:147-172.

Soltis J, 2004. Mating systems. In: Macaque societies: a model for the study of social organization (Thierry B, Singh M, Kaumanns W, eds). New York: Cambridge University Press; 135-151.

Soltis J, Thomsen R, Takenaka O, 2001. The interaction of male and female reproductive strategies and paternity in wild Japanese macaques, Macaca fuscata. Anim Behav:485–494.

Sprague DS, 1998. Age, dominance rank, natal status, and tenure among male macaques. Am J Phys Anthropol 105:511-521.

Stuart-Fox DM, Firth D, Moussalli A, Whiting MJ, 2006. Multiple signals in chameleon contests: designing and analysing animal contests as a tournament. Anim Behav 71:1263-1271.

Syme GJ, 1974. Competitive orders as measures of social dominance Anim Behav 22:931-940.

Taub D, 1980. Female choice and mating strategies among wild Barbary macaques (Macaca sylvanus L.). In: The macaques: Studies in ecology, behavior and evolution; 287-344.

Thierry B, in press. The macaques: a double-layered social organization. In: Primates in Perspective 2nd Edition, 2 ed (Campbell C, Fuentes A, MacKinnon KC, Panger M, Bearder S, eds). Oxford: Oxford University Press.

Tomasello M, Call J, 1997. Primate cognition. New York: Oxford Univ Press.

van der Dennen JMG, 1995. The origin of war: the evolution of male-coalitional reproductive strategy. Groningen: Origin Press.

van Hooff J, van Schaik CP, 1992. Cooperation in competition: the ecology of primate bonds. In: Coalitions and alliances in humans and other animals (Harcourt AH, de Waal FBM, eds). Oxford: Oxford University Press; 357-390.

van Noordwijk MA, van Schaik CP, 2001. Career moves: Transfer and rank challenge decisions by male long-tailed macaques. Behaviour 138:359-395.

van Noordwijk MA, van Schaik CP, 2004a. Sexual selection and the careers of primate males: paternity concentration, dominance-acquisition tactics and transfer decisions. In: Sexual selection in primates: New and comparative

perspectives (Kappeler PM, van Schaik CP, eds). Cambridge: Cambridge University Press; 208-229.

van Noordwijk MA, van Schaik CP, 2004b. Sexual selection and the careers of primate males: paternity concentration, dominance-acquisition tactics and transfer decisions. In: Sexual selction in primates: new and comparative perspectives (Kappeler PM, van Schaik CP, eds). New York: Cambridge University Press; 208-229.

van Schaik CP, 1996. Social evolution in primates: the role of ecological factors and male behaviour. Proceedings of the British Academy 88:9-31.

van Schaik CP, Pandit SA, Vogel ER, 2004a. A model for within-group coalitionary aggression among males. Behav Ecol Sociobiol 57:101-109.

van Schaik CP, Pandit SA, Vogel ER, 2006. Toward a general model for male-male coalitions in primate groups. In: Cooperation in primates and humans (Kappeler PM, van Schaik CP, eds). Berlin: Springer; 143-163.

van Schaik CP, Pradhan GR, van Noordwijk MA, 2004b. Mating conflict in primates: infanticide, sexual harassment and female sexuality. In: Sexual selection in primates: new and comparative perspectives (Kappeler PM, van Schaik CP, eds). Cambridge: Cambridge University Press; 131-150.

Wall L, Christiansen T, Orwant J, 2000. Programming Perl. Sebastopol: O'Reilly.

Wallner B, Mostl E, Dittami J, 2007. Chronic levonorgestrel treatment in Macaca sylvanus: effects on perineal swelling size and fecal sex steroid excretion. Neuroendocrinology Letters 28:326-332.

Watts DP, 1998. Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. Behav Ecol Sociobiol 44:43-55.

Whitehead H, Connor R, 2005. Alliances I. How large should alliances be? Anim Behav 69:117-126.

Witt R, Schmidt C, Schmitt J, 1981. Social rank and darwinian fitness in a multi-male group of Barbary macaques (Macaca sylvana Linnaeus, 1758). Dominance reversals and male reproductive success Folia Primatol 36:201-211.

Wrangham RW, 1982. Mutualism, kinship, and social evolution. In: Current problems in sociobiology (Group KsCS, ed). Cambridge: Cambrige University Press; 269-289.

Zabel CJ, Glickman SE, Frank LG, Woodmansee KB, Keppel G, 1992. Coalition formation in a colony of prepubertal spotted hyenas. In: Coalitions and alliances in humans and other animals (Harcourt AH, de Waal FBM, eds). New York Oxford University Press; 233-257.

Zeh JA, Zeh DW, 2001. Reproductive mode and the genetic benefits of polyandry. Anim Behav 61:1051-1063.

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